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1.—Man the destroyer: late Quaternary changes in the Australian marsupial fauna

Presidential Address, 1967

by D. Merrilees*

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Abstract

Many species of large Australian marsupials appear to have become extinct in late Quaternary time, and this extinction is often ascribed to a mid-Recent episode of devastating aridity. Independent evidence of such an episode appears weak. An alternative reason for the marsupial extinction is modification or destruction of habitats by man-made fires. Man was present in Australia along with many marsupial species now extinct; new evidence of this association is presented for the Western Australian localities Billabalong (middle Murchison River), Wonberna and Guralia (near Balladonia), and Devil's Lair (Cape Leeuwin-Cape Naturaliste region). Australian Aborigines used fire freely, and repeated burnings probably had marked effects on plant ecosystems.

Western Australian marsupial-bearing deposits are reviewed. All appear to be of late Quaternary age. Species by species extinction over late Pleistocene and early Recent time appears to be characteristic of the Cape Leeuwin-Cape Naturaliste region. Other regions are not well known, but their fossil record is consistent with gradual impoverishment of the marsupial fauna. Such impoverishment may be due to repeated firing of the bush. Further investigation is needed to demonstrate this.

Introduction

In course of an examination of Western Australian deposits containing Quaternary fossil marsupials, and comparative material from other parts of Australia, I have had to consider a general question often posed, namely what was the fate of the Quaternary "giant" mammals. I have seen no indication in the Western Australian record that species of large marsupials have been replaced by smaller but otherwise similar species (as described by Cooke in Howell and Bourlière 1963) and little indication of intraspecific diminution in size (as described by Kurtén and Rausch 1959 or Wright and Lundelius 1963). Rather, it appears simply that there once lived in Western Australia species of marsupials, some very large, which have become extinct.

Of numerous hypotheses advanced to account for extinction of large Quaternary mammals, perhaps the most widely adopted relate extinction to climatic change. For Australia, the climatic episode usually singled out is the "Great Australian Arid Period" (Crocker and Cotton 1946 p. 79). However, there appear to be weaknesses in the concept of devastating aridity in southern Australia between 6,000 and 4,000 years ago (the dates given by Gill 1955b), and I have been led to reconsider the main alternative hypothesis, relating mammal extinction to human intervention (Tindale in Keast, Crocker and Christian 1959). It is suggested below that modification or destruction of marsupial habitats by man-made fires has resulted in extinction of many species of marsupials in prehistoric time.

There appears to be no stable list of names for marsupial taxa, and in particular macropodid nomenclature is very confused (Calaby 1966, Kirsch and Poole 1967). In general, I follow the names and generic concepts used in a survey of modern Australian mammals by W. D. L. Ride and E. Fry (in preparation). Specimen numbers are those of the appropriate collection in the Western Australian Museum unless otherwise indicated. Most of my studies relate to species of marsupials of size about equal to the introduced rabbit, or larger, and the term "larger marsupials" below should be taken to cover these species. In Figure 3 the chronology for the Würm Glaciation is based on van der Hammen, Maarleveld, Vogel, and Zagwijn (1967), Vogel and van der Hammen (1967), and Shotton (1967).

Although discussion of destructive attacks on the Australian marsupial fauna in historic time (Marshall 1966) could be given under the title used, attention is concentrated on prehistoric time.

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The "Great Australian Arid Period"

Crocker (1946) shows that calcareous hardpans are characteristic of the "mallee" (solonized brown) soils widespread in South Australia, even over non-calcareous bed rock, and suggests that the finer fractions of shell sand exposed during glacio-eustatic low sea levels, winnowed by high winds and blown far inland, are the source of most of this calcareous soil material. In regions of moderate to low rainfall, this calcareous loess is conceived as leached and re-deposited to form an illuviated hardpan B horizon, leaving a decalcified A horizon, largely siliceous. Crocker postulates a period of severe aridity with widespread devegetation, exposing these decalcified upper soil horizons to deflation, with the production of sand sheets and sand ridges. (He suggests that the siliceous sands of the coastal plain near Perth are, at least in part, the decalcified A horizons of coastal calcareous dunes, the illuviated lower portions of which are now the aeolianites of the "Coastal Limestone".)

Crocker (1946) links crustal movements in the Gulf region of South Australia with the absence of calcareous aeolianites from northerly portions of the region and with supposed warmer marine conditions indicated by *Anadara trapezia* to suggest that his postulated period of severe aridity is of mid-Recent age. In an addendum, Crocker (1946) accepts the postulate of Browne (1945) that many aspects of the Quaternary, including extinction of the characteristic Pleistocene suite of large marsupial herbivores, are related to relatively sudden replacement of humid by arid conditions in Australia, in turn related to deglaciation in high latitudes.

Gill (1955b) suggests that a post-glacial temperature maximum, widely accepted for the northern hemisphere, was registered also in Australia, and in south eastern Australia was accompanied by aridity, between about 6,000 and 4,000 years B.P. According to Gill (1955b, c), a radiocarbon date on *Coxiella* shells shows that the Chocolyn Silts at Lake Colongulac, western Victoria, and the fauna of large extinct marsupials represented in them, are of terminal Pleistocene age; they represent a time of high water level in the lake. Subsequently, there was a period sufficiently arid to dry up the lake and permit deflation of the lake floor to produce the Colongulac Loess, and later still, another period of high lake levels. Gill (1955b) correlates the Colongulac Loess with his "Postglacial Thermal Maximum", though radiocarbon dates apparently are not yet available to confirm this (Dury 1964, 1966a).

Many writers, including Gentilli (1949), Baur (1957), several contributors to Keast, Crocker and Christian (1959), Burbidge (1960), Moore (1964), and Mayr (1966) have used the concept of a mid-Recent aridity in Australia to account for phenomena they describe, but have not brought forward positive evidence (a) that a marked change from pluvial to arid conditions was registered for any part of Australia in late Quaternary time and (b) that this marked change was a mid-Recent event.

There have been few examinations of proven terminal Pleistocene and Recent stratigraphic sequences sufficiently detailed to be capable of providing such positive evidence, and one of the few (Mulvaney and Joyce 1965) suggests a different Recent history.

Mulvaney and Joyce (1965) show for Kenniff Cave (Queensland) that there was a slow rate of deposition (about half an inch per century) from about 16,000 years B.P. to about 10,000 years B.P. (i.e. terminal Pleistocene). From about 10,000 to about 5,000 years B.P. (earlier Recent) there was almost no deposition. From about 5,000 years B.P. up to modern times (later Recent), the rate of deposition was about one inch per century. There was no evidence of removal of fallen material from the cave floor by water wash, and deposition rates appeared to be a function of moisture supply to the roof and walls of the cave, and possibly also of human occupation. Mulvaney and Joyce suggest that the terminal Pleistocene in the Kenniff Cave area was relatively dry, the earlier Recent very dry, and the later Recent relatively wet.

The 10,000 to 5,000 year B.P. arid period of Mulvaney and Joyce (1965) is stated by them to be a period of desertion of Kenniff Cave, though there is an unexplained peak in the carbon and phosphorus concentration of floor deposit about half way through the arid period (Fig. 3b, op. cit.). At another site (The Tombs) within 20 miles of Kenniff Cave, a similar period of desertion of a site which was occupied before and after the early Recent is reported by Mulvaney and Joyce (1965), and is also suggested to represent a time of aridity.

Thus, Mulvaney and Joyce (1965) postulate a climatic deterioration during the latter part of the Pleistocene, culminating in an early Recent aridity with subsequent amelioration, but not a catastrophic onset of aridity in mid-Recent time like that of Crocker (in Keast, Crocker and Christian 1959).

Since the pioneer studies of Crocker (1946), detailed soil studies in circumscribed areas (e.g. van Dijk 1959, Wright 1962, Churchward 1963) have stressed multiplicity in soil-forming processes. Many such studies have followed Butler (1959) in his "K-cycle" concept of alternation between instability (destruction or burial of old soils) and stability (soil development), but few have proposed an absolute chronology for the cycles established. However Bowler and Harford (1966) do establish a chronological framework for events in the Echuca district, Victoria, and they suggest a complex history even for later Recent time.

According to Bowler and Harford (1966), there was tectonic activity in the Echuca region in early Recent time, and the first depositional event after this is dated (on "redistributed charcoal fragments . . . from laminated organic lacustrine silts . . .") at $6,800 \pm 150$ years B.P. (N — 152). Since this time (i.e. beginning only a few hundred years before the "Great Australian Arid Period" according to Gill 1955b) a complex sequence of events has included prior stream deposition, lake-lunette formation and ancestral river activity, "some of which were due to climatic changes the exact nature of which are not yet clear". Bowler and

Harford (1966) claim that the "tendency to appeal prematurely to climatic catastrophism, to invoke categorical arid-pluvial solutions, often obscures rather than clarifies the problems".

Partridge (1967) reports the presence in Murra-el-elevyn Cave, Nullarbor region, of a thylacine (specimen 64.8.1) for which a date on its desiccated soft tissues is given as $3,280 \pm 90$ years B.P. (GaK—693). Other "Bassian" taxa are present in surface litter in southern Nullarbor caves (see below). These too are likely to be of mid or later Recent age. If so, it is difficult to reconcile their presence with a catastrophic aridity in mid-Recent time, ending as late as 4,000 years B.P. (Gill 1955b). The mid-Recent aridity is sometimes regarded as so devastating as to have caused the extinction of numerous marsupial taxa as well as other animals and many plants over much of the continent. If so, and if the Nullarbor is, as suggested by Main, Lee and Littlejohn (1958), Gentili (1961), and others, a climatically sensitive or vulnerable region, one would not expect it to have been re-colonized by Bassian forms only a few hundred years after its devastation by aridity.

Gill (1955b) and many other proponents of a Recent thermal maximum in Australia (whether or not arid) link this episode with a similar episode reported for the northern hemisphere (often called the "altithermal" or "Climatic Optimum", e.g. Oakley 1964). But it should be noted that agreement on the character of this "Climatic Optimum" is far from unanimous. For example, Martin (1963) and Martin and Mehringer (in Wright and Frey 1965) state that pollen analyses in the arid south west of the United States of America do not support the concept of an "altithermal drought"; Wendorf (1961) reviews several lines of evidence, mainly fossil pollen, suggesting that there has been a decline in rainfall over the whole of post-Glacial time in the Llano Estacado region of south-western U.S.A. Over the last 6,000 to 7,000 years, according to Wendorf (1961), the climate became consistently and increasingly arid, although several minor relatively moist fluctuations are reflected in pollen spectra, and closely corresponding changes in evaporation rates are reflected in varying grain size in gypsum sediments.

On the other hand, Kottowski, Cooley and Ruhe (in Wright and Frey 1965) accept an arid "Altithermal" phase for a large area in south-western U.S.A., including the Llano Estacado, and Smith (in Wright and Frey 1961) accepts an arid "Xerothermic Interval" for a much more extensive part of North America, but in neither case is supporting evidence detailed. Indeed, Smith (op. cit.) expresses surprise that midden and cave remains, known in considerable detail and abundance in North America, fail "to corroborate the climatic chronology outlined" by him. Fock (1966) claims there have been "no drastic climatic changes" in the northern Cape Province, South Africa, in Recent time. Zeigert (1965) reports desiccation continuing up to historic time in the central Sahara, interrupted by a short wet subphase approximately in the 4th millenium B.C.

Galloway (1965) presents an interpretation of late Quaternary climate in Australia which does not make the common association (e.g. Broecker in Wright and Frey 1965) of high latitude glacial with middle latitude pluvial conditions. From studies of periglacial solifluction deposits and snowlines in south eastern Australia, and of lacustrine deposits at Lake George, near Canberra, Galloway (1965) concludes that the last glaciation of the Tasmanian and Kosciusko highlands was accompanied by a cold, windy, but rather dry climatic regime in adjacent unglaciated regions, and that the windiness extended far inland, producing the great sand ridges characteristic of central Australia. Under such a regime, rivers would flow and lakes fill from precipitation considerably less than at present, giving an impression in the geological record of "pluviation" (cf. von Wissman in Thomas 1956, Patton 1963). Lake George, for example, was about 40 feet deep, at least twice its present normal depth, some 15,000 years ago (Galloway 1967) under a rainfall probably substantially less than at present (Galloway 1965).

There is, according to Galloway (1965), little evidence of association of increased rainfall with episodes of higher temperatures in Australia, but he cites evidence for such an association for latitudes in North Africa and the Middle East comparable with those he studies in Australia. Thus, as Gill (1955b) points out, association of drought with high temperature should not be assumed (cf. Huzzayin in Thomas 1956, Poynton 1962, Butzer in Howell and Bourlière 1963, Ridder 1965).

Salmi (1955) reports marked deficiency of copper and cobalt in dung attributed to the giant ground-sloth *Myodon darwini*, and suggests this deficiency was the root cause of extinction of these and possibly other herbivores in Fuego-Patagonia in early Recent time. He suggests further that the mineral deficiency may be related to aridity or even to change from well distributed to markedly seasonal precipitation, resulting in copper and cobalt compounds in the soil becoming less available to plants, and hence to herbivores.

One possible source of error in conceiving a sudden onset of aridity as a cause of extinction in large mammals is the implication that sudden reduction in lushness of vegetation is equivalent to deterioration in food supply for large herbivores. It would appear that under existing conditions, the regions of greatest lushness of vegetation are not those supporting the greatest biomass of large herbivores. According to Bourlière (in Howell and Bourlière 1963), the African savannas, which are anything but "lush" in the conventional meaning, carry a far greater biomass of large mammals than any other African environment; he contrasts the Serengeti plain (c. 5,000 kg. ungulate per sq. km.) with a forest reserve in Ghana (5 kg. ungulate/ sq. km.) Bourlière mentions even more extreme differences than these, but points out that biomass calculations for managed reserves (in which study is easier than of the wild) may be misleading about natural conditions.

Bourlière (1965) mentions decline in numbers of topis and Uganda kobs in the Albert National Park (Congo) with restriction of bush fires, and an increase in these two species in the same area later as the tree cover was reduced by increasing numbers of elephants and buffaloes.

Studies on the ecology of the elephant, hippopotamus and rhinoceros may provide guides to the ecology of *Diprotodon* and *Zygomaturus* in Western Australia. It is not known whether *Diprotodon* and *Zygomaturus* were "amphibious" like the hippopotamus, though the curious narial structures of the marsupials suggest this. If they were not amphibious, then presumably they were plains wanderers like the elephant or the rhinoceros. It appears from the biomass calculations of Bourlière (1965) that either hippopotamus (south of Lake Edward) or elephant + rhinoceros (Garamba) can greatly outweigh other herbivores in short—or tall—grass tropical savanna, and can build up very large populations; by analogy, it is possible that *Diprotodon* and *Zygomaturus* could have colonized large areas of shrub steppe, scrub, savanna and savanna woodland in Western Australia. It is possible that the remains of shrubby plants in the gut or faeces of *Diprotodon* in the Lake Callabonna region (Stirling 1900) represented the normal diet of the animals concerned and not (cf. Gentilli 1961) a last resort in a time of deteriorating climate.

If this African experience can be transferred to south western Australia, it would seem possible that reduction in rainfall below the present level could actually increase the carrying capacity for large herbivores of the Cape Leeuwin-Cape Naturaliste region, which at present carries dense forest. Any general reduction in rainfall recorded in the southern part of Western Australia might at the same time transform other large areas from steppe to desert, with consequent overall reduction in total biomass of large herbivores, though a single fossil sample in the extreme south-west might show an increase.

Caution would seem necessary in interpreting one or a few fossil deposits in terms of changing rainfall, and in the particular problem of why there was an impoverishment of the larger marsupial fauna in late Quaternary time, there is at least one alternative to a "great aridity", namely human intervention.

Man-made fire and vegetation

There has been some suggestion, not generally accepted, that the Australopithecines used fire, but according to Oakley (1956, in von Koenigswald 1958, 1964) the use of fire was certainly known to Lower Palaeolithic man in China as early as Mindel (Elsterian) time, and in Europe as early as the "Great" Interglacial. West and McBurney (1955) describe deforestation at Hoxne, Suffolk, probably due to fire, possibly man-made, during the "Great" Interglacial. Hearths appear "with dramatic suddenness" in the Middle East (cf. Neuville 1931) and in Africa (Oakley 1964) in very late Acheulian cultures. There is "no doubt that

Neandertalers and Cro-magnons were fire-producers, with fire-making devices as part of their essential equipment" in Würm time (Oakley in von Koenigswald 1958).

Iversen (1956) has shown that Neolithic axes are effective in clearing forest, but has shown that fire is necessary to maintain forest clearings and to grow crops effectively in such clearings (Iversen 1949, 1956, 1960). Many others (e.g. Darby in Thomas 1956, Butzer 1964) have described or reviewed significant effects on plant, particularly forest, communities by Upper Palaeolithic peoples in Eurasia.

In high latitudes, it is not easy to disentangle evidence of climatic effects on plant systems from prehistoric human effects (Walker 1966a), or to assess the relative importance of man-made fires (Narr in Thomas 1956). In middle latitudes, fire may not be the main factor in human modifications of plant systems (Sauer in Thomas 1956, Stamp 1961), though there is a common opinion that human effects have been marked—e.g. "climate is not the cause of but only the condition under which deserts originate" (van Steenis 1936). Stewart (in Thomas 1956) gives a comprehensive review of the effects of man-made fires on vegetation patterns, including the statement "In summarizing the effect of fire on the North American grassland, it seems reasonable to assume that, since the moist prairies can support true forests and the dry plains can support xeric brush and scattered trees, and since the trees are capable of invading the sod, some non-geographic force is critical for the formation and maintenance of grasslands in America. Fires set by man have been present for thousands of years, and lightning-set fires have been rare. Burning by primitive peoples may thus be considered a determining factor". Cumberland (1962) claims that the human use of fire to hunt moas produced major changes in the vegetation and soils of the South Island of New Zealand.

In the humid low latitudes, however, climate may have been relatively stable (Sauer 1958) through the glacial waxings and wanings which had profound effects in high latitudes, so that human effects on plant systems are more readily discernible in low latitudes. There is abundant evidence that such effects have been marked, in particular that most tropical grasslands are anthropogenic. The "shifting cultivation" methods of many human communities of the low latitudes, involving clearing of forest, burning, cultivation and stock raising, are believed to deflect plant successions from climatic into biotic climax on a large scale (Bartlett in Thomas 1956, Richards 1957, Whyte 1957, Holmes 1958, Sauer 1958, Fosberg 1960, most contributors to Symposium 1960, Walker 1966b.)

King (1963) assembles accounts by Dampier, Cook, Phillip, Mitchell and other early European observers of extensive fires in many parts of Australia. Herbert (1938) describes and figures grassy areas up to several hundred acres in extent interspersed with rain forests in the Bunya Mountains, southern Queensland, shows that these areas have in the past supported

trees and will now support trees planted there, and suggests that they represent patches originally of forest fired by Aborigines. Wallace (1966) suggests that fires begun accidentally as well as deliberately by prehistoric Aborigines were common in the jarrah forests of south-western Australia. Meggitt (in Symposium 1960, p. 366) speaks of the "peripatetic pyromania" of Aboriginal groups in the arid central region of Australia, ranging over tens of thousands of square miles and setting fire to the scrub as they moved.

Cleland (1940, 1957) suggests that Tasmanian and South Australian Aboriginal groups produced only minor changes in vegetation patterns by their use of fire, but (in Cotton 1966) suggests that mulga scrub may have been replaced by porcupine grass or "spinifex" over large areas of Central Australia as a result of repeated firing. Gilbert (1959) and Davies (1964) suggest that Tasmanian man-made fires prevented rain forest from invading sclerophyll forest in several areas, and that the sedgeland or "button-grass plains" so characteristic of the Tasmanian highlands replaced burnt rain forests. Jones (1966) reviews evidence that the Tasmanian west coast sedgeland was maintained by "intense aboriginal fire pressure". According to Meston (1949) fewer than 2,000 Tasmanians lived on the island at the time of the European invasion. Thus, a very small human population with a limited technology can be conceived as affecting the plant cover over some substantial proportion of an area of over 25,000 square miles. Meggitt (in Symposium 1960) suggests that even smaller groups may modify the plant cover of even larger areas in central Australia. Such modification could be profound even if burning operations were controlled as carefully as in the cases cited by Nind (1832), Thomson (1949) and Gardner (1957).

Eiseley (1946) and others have raised objections to the hypothesis that the use of fire by prehistoric man in North America has played a major part in the late Quaternary extinction of large mammals there. But in Australia, especially in regions with marked summer drought, it appears reasonable to postulate marked effects on plant ecosystems by fire (Coaldrake 1951; Gardner 1957; Specht, Rayson and Jackman 1958). Wallace (1966) points out that lightning starts substantial numbers of fires in the jarrah forests of south western Australia, and no doubt this applies elsewhere. Nevertheless, deliberate and frequently repeated firing of vegetation by man can reasonably be conceived as a new dimension in plant geography after the first invasion of Australia by man. I postulate that long-continued firing of the bush had profound effects on the mammalian fauna of Australia. These effects should be discernible in, and only in, late Quaternary time.

Man and the late Quaternary extinction of mammals outside Australia

North America

Lance (1955), Neill (1957), Jelinek (1957), Martin (1963, 1966 and in Hubbs 1958), Hester

(1960-61), Romer (in Nairn 1961), Mason (1962), Shutler (1965) and others have reported or reviewed associations of extinct mammals with prehistoric man in North America, and most of these writers have suggested that man was the agent of extinction. The chronology of the North American extinction is examined critically by Hester (1960-61).

In at least one region the first appearance of man is followed immediately by some mammal extinction, namely in the Llano Estacado and Monahans Dunes regions of south western U.S.A. Wendorf (1961) reviews evidence from pollen, diatoms, molluscs, evaporites, dune stratigraphy and soils of an alternation of wetter and drier climatic phases. Mammal- and artefact-bearing deposits are correlated with this inferred climatic framework. None of the drier phases appears to have been catastrophically arid. Yet in one relatively short dry phase (the Scharbauer Interval) in a generally pluvial time (the San Jon Pluvial), the mammoth, horse, camel, peccary, and four-horned antelope appear to have become extinct in the region, though more than one species of bison survived. The earliest sign of human occupation dates from the preceding wetter phase (the Blackwater Sub-Pluvial).

Europe

Charlesworth (1957—Chapter 34) surveys a great deal of investigation into the abundance and times of appearance and disappearance of mammals once living in Europe, but now extinct there. Little pattern is discernible in Charlesworth's survey, but rather there appears to be great variation in the time of disappearance of different species from different regions. According to Butzer (1964), evidence of any marked human effects on these mammalian extinctions is inconclusive.

Africa

Martin (1966) discusses an apparent anomaly in the case for man as the extinctive agency in the late Quaternary loss of large mammals. That is the persistence to modern times in Africa of a very varied fauna of large mammals, along with early development there of man. Martin points out that the present variety of large African mammals, great as it is, nevertheless is not as great as the variety existing in the Pleistocene up to early Würm time, that the wave of extinction is a later Pleistocene event in Africa, but not a terminal Pleistocene or early Recent event as in North America, and that the great African mammal extinction post-dates the widespread appearance of Acheulian artefacts in African deposits.

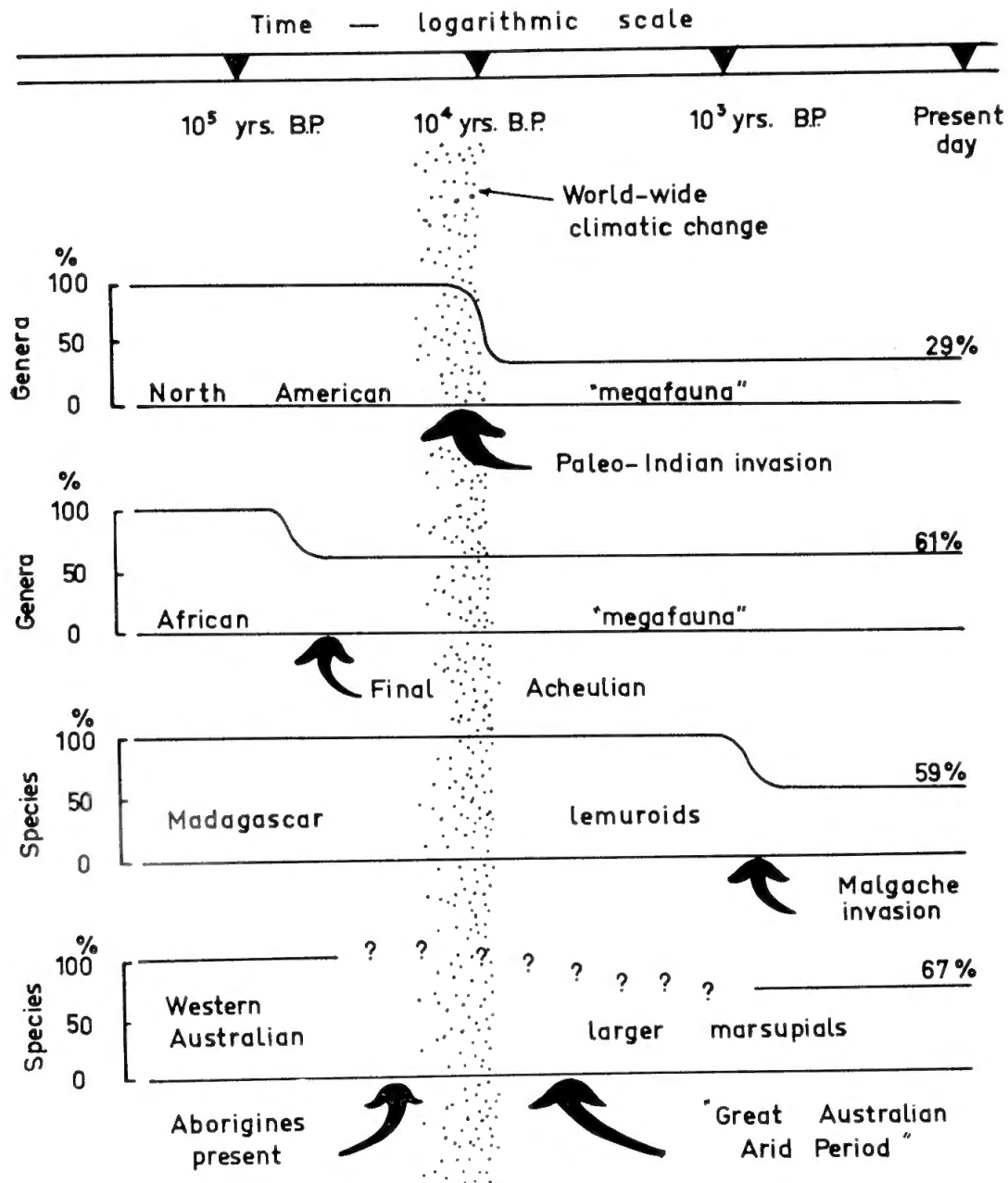
Martin (1966) suggests that lack of synchrony between the African wave of extinction of large mammals and the North American wave of extinction argues against climatic deterioration as the underlying cause of extinction, and that it is more consistent to relate this lack of synchrony to the lack of synchrony in human development in the two

regions. He reinforces this suggestion with the observation that extinction of lemuroids in Madagascar followed human invasion within the last 1,000 years (cf. Coon 1965).

Martin (1966) summarizes his case in a diagram; a slightly modified version of this, with the addition of Western Australian data, is here reproduced as Figure 1.

FIG.1 EXTINCTION CHRONOLOGY
OF LATE QUATERNARY MAMMALS

After Martin (1966, Fig.1) with addition of data from
Western Australia



Leakey (1966) points out that generic lists given by Martin (1966) are based on out-of-date taxonomic studies, and queries the body weight estimates for some taxa; Martin (1967) recalculates his survival and extinction rates and shows his original (1966) calculations to be of the right order. Leakey (1966) also criticizes Martin's use of a radiocarbon date of

58,000 years B.P. from carbonized wood, possibly contaminated by later waterlogging, at Kalambo Falls to date the final Acheulian in central Africa. But all that need be established is that fire-using man was present in central Africa before the extinction of the large mammals of the Olduvai Bed IV, Olorgersailie and other deposits mentioned by Martin.

Leakey does not discuss this, but according to Oakley (1961, 1964), the "art of making fire" became known south of the Sahara only in the late phases of Acheulian development.

Leakey (1966, 1967) raises the question of how the earlier Palaeolithic men in central Africa can be conceived as devastating the large mammal fauna when their "Upper Palaeolithic, Stillbay and Mesolithic" successors, in greater numbers and with better hunting equipment, had little effect on the surviving fauna. If it is the use of fire, not hunting, that is critical for the large mammals, and if small numbers of men can produce large scale effects by firing vegetation over large areas, improved hunting techniques and equipment can be conceived as a response to, rather than the cause of, widespread extinction of species of game animals.

New Zealand

There is an interesting parallel between man as a mammal-destroyer in many regions, and man as the bird destroyer in New Zealand before the introduction of mammals (Duff 1956, Cumberland 1962).

Special characteristics of the late Quaternary extinction of Mammals

According to Martin (in Hubbs 1958) one of the noteworthy characteristics of the late Quaternary extinction of large mammals in North America is that it was extinction without replacement by related taxa. He gives the horses as an example. "Through the Cenozoic, equid genera disappear; *Hyracotherium* and others in the Eocene; *Meshippus* in the Oligocene; *Miohippus*, *Parahippus* and others in the Miocene; *Calippus*, *Hipparion*, etc. in the Pliocene; and *Nanippus* and *Plesippus* in the early Pleistocene. They represent a record of replacement by morphologically modified and adaptively improved types of horses. In the late Pleistocene, the extinction of the North American *Equus* and South American *Equus* and *Hippidion* is not an equivalent event for it constitutes extinction without replacement. For perhaps 3,000 to 6,000 years in the Americas the horse was absent. Following post-Columbian reintroduction, feral horses reoccupied grassland habitats with unseemingly haste. Darwin reported that they spread from Buenos Aires to the Straits of Magellan, 1,300 miles, in 43 years."

Martin (in Hubbs 1958) also suggests that the late Quaternary wave of mammal extinctions was more intense than any previous Quaternary wave, and the Quaternary extinctions more intense than the Tertiary. See also Simpson (1947) and Kurtén (1966). To what extent this apparent effect is due to the late Quaternary being better known than the early Quaternary, and the early Quaternary better known than any part of the Tertiary, is not discussed.

Another special feature of the late Quaternary mammal extinction, according to Martin (in Hubbs 1958) is differential loss of the larger kinds as compared with the smaller.

Because of these features of the late Quaternary mammal extinction, and the lack of evidence of major climatic change during the North American extinctions studied, Martin (in Hubbs 1958) concludes: "It would appear that within the Cenozoic, the late Pleistocene environment had some unique features. Man is the only one clearly identified."

Eastern Australian associations of man with marsupials extinct on the mainland before European invasion

The basalt plains of western Victoria

Lake Colongulac (also called Lake Timboon in some early records) is described by Gill (1953b) as "the classic locality in Victoria for the extinct marsupial fauna". Gill (1953b) shows that the large extinct marsupial taxa occur in the Chocolyn Silts, and that these underlie deposits representing an episode of volcanic activity; deposits overlying the volcanic materials have also yielded fossil marsupials, but only of species still living. According to Gill (1953b) the bones in the Chocolyn Silts are reworked from an earlier deposit, so that he postulates a considerable interval of time between the Chocolyn Silts fauna and the post-volcanic fauna. He does not suggest that the volcanic activity had any more than local effects on the mammals, but postulates that during the interval in which the volcanic outbreaks occurred, there was also a marked faunal change. Consequently, when the Lake Colongulac area was repopulated by mammals, only living species were available for this repopulation. A metatarsal IV of a large macropodid from the Chocolyn Silts ("the Colongulac Bone" Spencer and Walcott 1911) shows cuts which Gill (1951, 1952, 1953b) considers to be man-made (cf. cuts on dugong bone, Etheridge, David and Grimshaw 1897). Gill (1953b) also suggests that the fragmentation and local concentration of bones of the Chocolyn Silts fauna are consistent with their being the debris of Aboriginal hunters' camps. Dog remains, taken by Gill (1953b) as presumptive evidence of human occupation of the Lake Colongulac area before or during the time of the Chocolyn Silts fauna, have been shown (see Mulvaney 1964b p. 431) to be of later age than the marsupials.

The evidence for association of man with extinct marsupials at Lake Colongulac remains, as Mulvaney 1964b points out, somewhat inconclusive. If man was present, he was a contemporary of *Thylacoleo carnifex* and species of *Diprotodon*, *Procoptodon* and *Thylacinus*, together with one or more of the large extinct *Macropus* species, and possibly others, by direct evidence from Lake Colongulac (Gill

1953b p. 35), and possibly also of a *Protemnodon* resembling *anak*, at least one nototherian, and *Sarcophilus*, if Gill (1953b) is right in equating other basalt plains finds with the Chocodyn Silts fauna of Lake Colongulac. They appear to be of very late Pleistocene age, $13,725 \pm 350$ years B.P. according to radiocarbon analysis of *Coxiella* shells from Lake Colongulac (Gill 1955c).

Pejark Marsh, near Terang, is another basalt plains site from which association of extinct marsupials with man is reported. According to Gill (1953b), Pejark Marsh shows a succession in which black sticky clay overlies a distinctively bright yellow clay. Bones of species of *Diprotodon*, *Palorchestes*, *Macropus* (resembling *titan*) and *Vombatus* are known, which are reddish in colour despite their occurrence at the base of the black clay. Gill (1953b) suggests that they have been let down from a pre-existing deposit on to an erosion surface, before being buried by the black clay, and that the bones represent dry climatic conditions, later replaced by wetter conditions represented by the black clay, which he interprets as a swamp fill. The evidence for human occupation is a single millstone, anvil or husking stone found (Spencer and Walcott 1911, Keble 1947) in the distinctive yellow clay below the bone horizon. Mulvaney (1964b) expresses no doubts that the specimen concerned (figured by Mahony 1943 Pl. 3) is indeed a used stone tool, but lays stress on the fact that the only evidence that the specimen came from the yellow clay is the original finder's assertion, and that such evidence is inadequate for a crucial issue. The issue no longer appears crucial, and the original finder's evidence as reported by Keble (1947 pp. 46-48) appears unequivocal; thus in the Pejark Marsh area man probably preceded species of *Diprotodon*, *Palorchestes* and *Macropus* which are now extinct. The age of the human occupation is estimated by Gill (1953b) as late Pleistocene or early Recent.

Keble (1947) reports association of an axe head, grooved for hafting, with marsupial bones in a terrace of the Merri River, near Bushfield, in the Warrnambool district. Gill (1953b) estimates the age of this association as late Recent, and establishes new sites for the mammal fauna, recognizable by their black coloration as well as by their stratigraphic occurrence, as equivalent to Keble's horizon. Wakefield (1964) has re-examined the Bushfield mammals and reports the presence of *Sarcophilus harrisi* and *Bettongia lesueuri*, both of which had disappeared from the basalt plains district before or during the earliest years of European occupation.

Gill (1953b, 1955c) reports a radiocarbon date of 538 ± 200 years B.P. for charcoal from an "aboriginal kitchen midden" on Koroit Beach, near the Tower Hill volcano in the Warrnambool district. This is reported (Wakefield 1964) to contain *Sarcophilus harrisi*.

Ballarat district, Victoria

The "Buninyong Bone", found in a mine near Ballarat, and thought to be part of *Diprotodon*

rib (Mahony 1943) shows cuts originally thought to be man-made, but this suggestion is rejected by Gregory (1904), Mahony (1943) and Mulvaney (1964b).

Port Augusta district, South Australia

Cooper (1959) reports finding teeth and bones, some of them charred, alongside large stone tools, on an eroded sand dune west of Port Augusta. The bones and teeth are attributed by H. H. Finlayson to a small species of *Diprotodon*, and the artefacts are attributed by Cooper to an early Aboriginal culture. The possibility is acknowledged that the teeth, bones and artefacts may not be contemporaneous.

The Murray Valley in South Australia

Hale and Tindale (1930) describe a site south of Swan Reach, South Australia, on the bank of Tartanga Lagoon, which lies alongside the channel of the Murray River. Human remains and artefacts were associated with marsupial remains representing species still living. About a mile further downstream, an excavation in the floor of a rock shelter near Devon Downs yielded a large quantity of artefacts, with some human bony remains, and (in layers VI, VIII, IX and possibly XII) remains of *Sarcophilus harrisi*. Other marsupial remains at various levels represented species still persisting on the Australian mainland. Hale and Tindale (1930) develop a concept of culture succession in the artefacts, later expanded by Tindale (1957, cf. Birdsall 1967): according to this scheme, *Sarcophilus* persisted in the Devon Downs district into the "Mudukian cultural phase", i.e. into the latter part of Recent time. (Mulvaney 1960 shows that the "culture succession" at Devon Downs may represent merely changes in technique, or changed emphases among one kind of people—cf. Yamaguchi 1967, but this does not affect the *Sarcophilus* date.) A recent re-examination of the mammal remains excavated from Devon Downs has shown that *Thylacinus* also was present, but at a time not recorded. (Wakefield in Mulvaney, Lawton and Twidale 1964.)

About 10 miles downstream from Devon Downs is a group of rock shelters known as Fromm's Landing 1, 2 . . . 6. Mulvaney (1960) reports an excavation in Shelter 2, Fromm's Landing; a later report (Wakefield in Mulvaney, Lawton and Twidale 1964) shows *Sarcophilus harrisi* to have been present in Levels 5 and 7, and *Thylacinus* sp. in Level 7, i.e. between 3240 ± 80 and 3881 ± 85 years B.P. (See also Macintosh & Mahoney—in Mulvaney, Lawton and Twidale 1964—on the thylacine.)

Mulvaney, Lawton and Twidale (1964) report an excavation in Shelter 6, Fromm's Landing, with an appendix by Wakefield, analyzing the mammal remains, and one by Macintosh, describing a dog skeleton, dated between 1950 ± 91 and 3170 ± 94 years B.P., stated to be the "oldest genuinely dated dingo" (in Australia).

Lakes Menindee and Tandou, New South Wales

Tedford (1967) describes a fossiliferous occurrence at Lake Menindee, in south western N.S.W., superseding an earlier preliminary description (Tedford 1955). Lake Menindee is one of a chain of lakes near the Darling River, which intermittently discharges water into the lakes through distributaries. I have examined the Lake Menindee fossiliferous deposit only briefly, but have spent several days collecting from and observing deposits at another lake in the chain, Lake Tandou. The two deposits, although about 20 miles apart, are so distinctive and so similar that I assume they were laid down at the same time under the same conditions.

In each case the fossiliferous deposit consists of a narrow ridge encircling the smoothly rounded margin of a lake bed several miles in diameter. Tedford (1967) concentrated attention on the northern portion of the ridge encircling Lake Menindee, while I concentrated on the eastern portion of the Lake Tandou ridge; he suggests that the structure of the western portions may differ from that of the eastern. The two areas examined both contain a core of pale grey or greenish material making up the greater proportion of the ridge, with an overlying but thinner band of bright brick red colour, overlain in turn by sand, much of it mobile, but much fixed under a plant cover. Tedford (1967) concludes from petrographic studies of the Lake Menindee deposits that the pale and the bright red materials are different phases of a single deposit of wind-blown fine sand, and that the colour difference, which is very striking in the field, is due merely to the masking of the red colour at lower levels by calcareous deposition. The uppermost sand is a young deposit resulting from deflation of the grey and red material. The lower pale material and its red capping are interpreted (Tedford 1967) respectively as the B and A horizons of a soil profile developed in a wind-blown deposit.

Petrographic evidence independent of fossil evidence, that the ridges bordering Lake Menindee (and presumably also Lake Tandou) are of sub-aerial origin is valuable because the fossils include remains of aquatic animals (fish, crustaceans and bivalves) as well as terrestrial mammals, birds and reptiles, and these aquatic animals must have been transported either from the lake immediately adjacent, or from the Darling River or its distributaries a few miles away (see map, Tedford 1967 p. 8). At Lake Tandou, remains of aquatic animals are abundant, but the bivalves especially and the fish and crustaceans quite markedly, occur in local concentrations, each concentration apparently the feeding point of the predator concerned. Charred fish bone (67.7.3) suggests the food was cooked, so that man would appear to be the collector of this food. Some of the mammal remains (*Procoptodon goliah*, *Macropus ferragus* at Lake Menindee—Tedford 1955 and 1967—and wombat and bettong at

Lake Tandou) are also charred, and presumably also represent the remains of human meals—cf. Mitchell (1949).

Estimates of the age of two samples of charcoal, from the lower pale (B) part of the Lake Menindee soil profile, but near the A horizon, are reported by Tedford (1967)—26,300 \pm 1,500 years B.P. (LJ—204) and (cf. Tindale 1964) 18,800 \pm 800 years B.P. (GaK—335). Tedford suggests that the discrepancy between these dates may result from a slow rate of original aeolian deposition, implying that the two charcoal samples may have been stratigraphically separated in spite of their apparent similarity. If this is so, human occupation of the Lake Tandou site must be very old, because we found shell, presumably transported by man, at very low levels in the lower aeolian deposit at Lake Tandou, only a few feet (not measured) above the level of the lake floor, far below the contact with the bright red A horizon. A previous date of 6,570 \pm 100 years B.P. (NZ 66—Tindale 1957) on bivalve shell, also from the upper part of the B zone of the soil profile, is suggested by Tedford (1967) to represent a sample consisting partly of old shell and partly of modern shell, and to be inconsistent with the extinct mammal assemblage at Lake Menindee.

Forbes, New South Wales

Andrews (1910) reports that "Under the alluvium in Mr Hasemer's brickpit at Forbes, and at a depth of 18 feet below the surface, *Diprotodon* bones have been found in association with aboriginal ovens". However, Andrews later informed Mahony (1943) that he himself had not observed the association.

Wellington Caves, New South Wales

Mahony (1943) gives the history of the finding of an allegedly human molar tooth in fossiliferous deposits in Wellington Caves; Campbell (1949) shows that the tooth is not human, and Finlayson (1949) that it is *macropodid*.

Padypadiy, Northern Territory

Calaby and White (1967) describe an association of *Sarcophilus harrisi* with human occupational debris dated at 3120 \pm 100 radio-carbon years B.P. (A.N.U.—017).

Aboriginal oral traditions, rock carvings and paintings, various localities

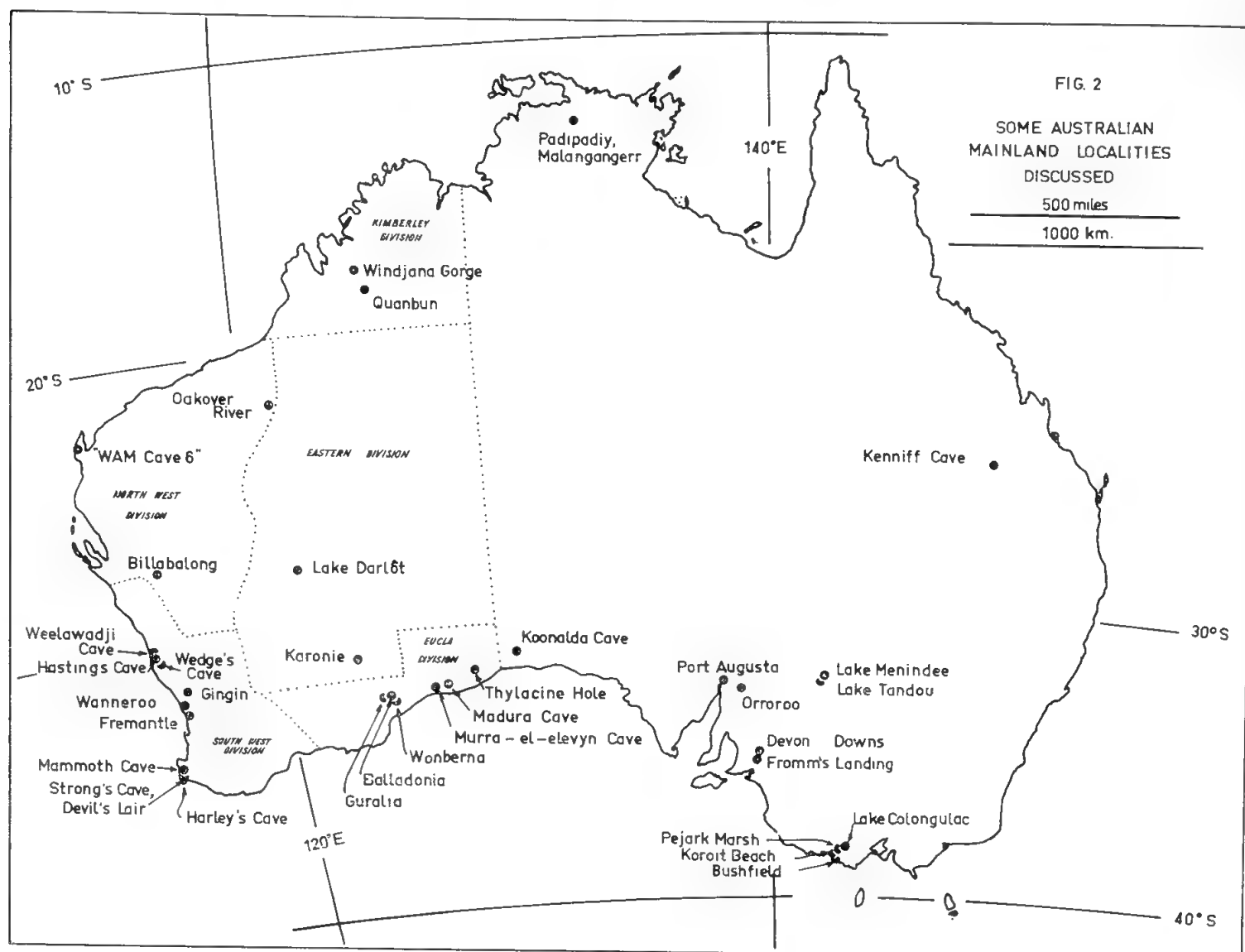
There are reports of association of Aboriginal man with animals now extinct (e.g. Tindale 1951, Mountford and Edwards 1962) based on artistic and oral evidence.

A preliminary review of marsupial-bearing deposits in Western Australia

Marsupial remains have been collected from at least 80 caves in the South West Division of Western Australia, and at least 30 caves in the Eucla Division. The sites of some of these caves are shown in Figure 2, along with other fossiliferous sites mentioned herein. Figure 3

includes Western Australian Quaternary deposits for which some information is available on geological age; there is no reason to suppose that any other marsupial-bearing deposit in

Western Australia is much older. It is hoped to publish more detailed studies of Western Australian marsupial-bearing deposits in due course.



Mammoth Cave

Mammoth Cave appears to be the existing remnant of what was once a longer and probably wider tunnel penetrating calcareous aeolianites occurring in the extreme southwestern portion of Western Australia. These aeolianites cap a ridge of Precambrian crystalline rocks forming the western wall of the southern Perth Basin (Lowry 1965). Similar aeolianites, lying on sediments of the Perth Basin, occur in a long narrow belt bordering the present western coast of Western Australia (McArthur and Bettenay 1960) and other coastal areas; they and associated marine sediments are known collectively as "Coastal Limestone" (Smith 1963).

Marsupial fossils were discovered in Mammoth Cave in 1904, and large quantities were collected between 1909 and 1915 by L. Glauert. Little remains of the deposit excavated by Glauert, but its position is known. Study of the remnants of this deposit, and of the few published and unpublished records of the excavator, show that the fossils were recovered from a relatively small volume of deposit, less than

15 ft. long, 12 ft. wide and probably less than 6 ft. thick, dipping towards the cave entrance. Glauert (1910) states that an older and a younger series of bony remains were collected but these are not now distinguishable in the Western Australian Museum collection. Glauert (1910) reports that a flowstone layer separated the two series, and that the whole deposit was covered by a flowstone layer.

E. L. Lundelius collected charcoal from the remnants of the Mammoth Cave deposit in 1954, and I collected a smaller sample in 1961; these samples have been dated as greater than 37,000 (date no. 0-657) and greater than 31,500 (Tx-31) years B.P. respectively. My charcoal sample probably represents only the upper few feet of the fossiliferous deposit, whereas that of Lundelius may represent most of its thickness, but probably the difference between the estimates means merely that one sample was larger, making possible the recording of a higher limiting date. For present purposes it is safe to assume that the upper parts of the Mammoth Cave marsupial-bearing deposit are older than 31,000 years B.P.

In order to estimate older age limits for this deposit, the following assumptions, on matters still debatable, are made. The Cape Leeuwin—Cape Naturaliste region is taken to have been tectonically stable over the last few glacial cycles (Lowry 1965, 1967). Glacio-eustatic correlation between this region and other distant regions of the northern hemisphere is made (Richards and Fairbridge 1965, Grindley 1967, Hoyt 1967). Early Pleistocene marine transgressions in excess of 40 metres above modern mean sea level (Butzer and Cuerda 1962, Stephens and Synge in Dury 1966b) are accepted as affecting the region. Wind-blown dunes of shell sand, not lithified, are assumed not to survive marine transgression, and lithified dunes to preserve traces of marine transgression. The interpretation by Butzer and Cuerda (1962, Fig. 10) of southern Mallorcan shorelines attributed to Hoxnian (—Hoxnian) and Eemian time is accepted.

On these assumptions, it would appear that the wind blown dunes of shell sand now represented by the aeolianites in which Mammoth Cave is cut are of post-Cromerian age. Crystalline rock basement is not exposed in Mammoth Cave, but is probably about 40 metres above modern mean sea level, and glacio-eustatic sea levels in excess of this appear not to be known from the Hoxnian or Eemian Interglacials, nor from any of the Mindel, Riss or Würm interstadials (Butzer and Cuerda 1962, Stephens and Synge in Dury 1966b). Cementation of the dunes, development in several stages of a cave within them, and accumulation of a fossiliferous deposit in this cave presumably occupied considerable time, so that it is probably safe to assume that the Mammoth Cave marsupial-bearing deposit is not older than later Middle (or even early Upper) Pleistocene, within any of the meanings of these terms tabulated by Butzer (1964 p. 28). See Fig. 3.

The fossiliferous deposit in Mammoth Cave was heterogeneous, containing bone, plant debris, snail shells, charcoal, soil, sand, and layers of flowstone (Glauert 1910) and also lumps of limestone (Glauert, unpublished notes preserved in Western Australian Museum library). Such a deposit is more consistent with a talus than with a water-laid origin, and the deposit appears to me to have been a mixture of material fallen from the ceiling of the cave, and through holes in the roof of the cave from the outside surface. I have been unable to find open holes in the existing roof, but there are deep soft patches in the surface slope roofing the cave in the vicinity of the fossiliferous deposit. Openings are visible in the ceiling which could correspond with these soft patches, so it is probable that these openings and soft patches are holes once penetrating the roof of the cave which are now blocked with plant debris and soil.

I have not found any Mammoth Cave fossils bearing "unmistakable evidence of water transport" (Glauert 1910) in the Western Australian Museum collection, but many specimens (e.g. *Setonix*, 65.1.4) are partly articulated, suggesting that the animals concerned were buried with the investing soft tissues intact. The oc-

currence of articulated skeletons not accompanied by water-worn bones is more consistent with a talus than with a water-laid origin for the deposit. So is the relatively steep dip, not recorded, but probably of the order of 15°.

Glauert (1910, 1912a, 1914, 1921b, 1926, 1948) published partial accounts of the Mammoth Cave fauna, and many later writers (e.g. Lundelius 1960, Cook 1963a, Tedford 1967) have copied Glauert's list with or without amendment. Studies of the Mammoth Cave specimens remain incomplete, but the following list of species present, based on independent work on these collections is given, despite its incompleteness, for reference in due course. The Western Australian Museum catalogue number is given for a least one specimen of the taxon concerned, in those cases marked *, the holotype.

The Mammoth Cave fauna

Marsupials

<i>Dasyurus geoffroyi</i>	66.7.13
Small dasyurids	66.9.7
<i>Sarcophilus harrisi</i>	66.9.15
<i>Thylacinus cynocephalus</i> —see Ride 1964	61.2.26
<i>Isodon obesulus</i> —see Merrilees 1968b	66.2.211
<i>Perameles</i> , of <i>bougainville</i> group—see Merrilees 1968b	66.2.184
<i>Trichosurus vulpecula</i>	66.9.21
<i>Pseudocheirus occidentalis</i>	66.6.24
<i>Thylacoleo</i> , species not known	64.10.24
<i>Phascolarctos</i> cf. <i>cinereus</i> (under review by B. Daily)	64.2.29
<i>Vombatus hacketti</i>	*60.10.3
<i>Potorous gilberti</i>	66.3.35
<i>Setonix brachyurus</i>	12030
<i>Protemnodon</i> cf. <i>brehus</i> (Tedford 1967 pp. 108, 109; see also Cook 1963a)	64.2.17
Wallaby resembling <i>Wallabia bicolor</i>	66.8.17
<i>Macropus irma</i>	66.9.30
<i>Macropus</i> cf. <i>eugentii</i>	66.9.28
<i>Macropus fuliginosus</i>	66.8.8
Large macropodine, similar in size to <i>M. fuliginosus</i>	66.9.50
<i>Sthenurus occidentalis</i> —see Merrilees 1968a	*60.10.2
<i>Sthenurus browni</i> —see Merrilees 1968a	*63.2.94
<i>Zygomaturus trilobus</i>	64.10.15

Non-marsupials

Monotremes—3 species (J. A. Mahoney, pers. comm.)	60.10.1
.....	61.6.4
.....	61.6.11
Murids	65.4.39
Bat	67.8.1
Bird, small species	67.7.1
Bird, large species	61.6.12
Snake, probably <i>Python</i> sp.	65.4.35
Gastropod, probably <i>Bothriembryon</i> sp.	61.273
Gastropod, a small species	with 66.9.55
Plants	Geol. Surv. West. Aust. 10088

This list includes some taxa not previously reported, and omits taxa previously reported, but for which there appear to be no supporting specimens (*Palorchestes*, *Macrotis*, *Bettongia*) or which have no biological meaning (*Phascolomys parvus*—see Merrilees 1968c).

Like most other caves in the vicinity, Mammoth Cave is abundantly littered with bones lying on exposed surfaces, presumably the remains of animals of the recent past. Glauert (1948) reports both *Bettongia lesueuri* and *B. pencillata* from "Mammoth Cave", but I can find no specimen of the former, while specimens of the latter (66.9.26, 27) show a mode of preservation more consistent with surface litter than with the excavated deposit. A single dog tooth (now 67.1.47), lacking catalogue number or label, lay in a drawer in the Museum labelled "Mammoth Cave", alongside specimens bearing

matrix characteristic of the excavated deposit. The dog tooth carries no such matrix, and its appearance and colour are more consistent with surface litter than with excavated material. In view of this, and of the absence of dog remains anywhere else known to be older than about 3,000 years B.P. (Macintosh in Mulvaney, Lawton and Twidale 1964), I have not included *Canis* in the faunal list above.

Strong's Cave

Strong's Cave is discussed by Cook (1963a) and Lowry (1965). It is about 7 miles south of Mammoth Cave, and consists of a long tunnel in the bottom of which a small stream flows in a south-westerly direction. This stream is incised into crystalline basement rock, and its banks in most places consist of siliceous sandy material containing large (1 ft or more diameter) water-born boulders, usually very sparsely distributed through the sand. Teeth of sharks, rays and teleosts (66.5.23, 65.6.55, 65.9.7 etc.) occur in the sand. Most of the walls and the roof of the cave appear to consist of aeolianites or of well-cemented fossil soils. It appears that crystalline basement in this area is overlain by a sea beach deposit, upon which wind-blown dunes of shell sand were piled in at least two episodes separated by a period of soil formation.

The deposit of sand with fish teeth and boulders exposed in Strong's Cave, which I interpret as a beach deposit, lies about 30 metres above modern mean sea level. On the same assumptions as made for Mammoth Cave, it may be suggested that the immediate vicinity of Strong's Cave was submerged in Hoxnian ("Great") Interglacial time, and that accumulation of dunes, cementation, soil formation, cave formation and accumulation of marsupial-bearing deposits in the cave could not have begun before this time. Like Mammoth Cave, Strong's Cave appears to have had a complex developmental history, and this history could have begun one whole glacial cycle behind that of Mammoth Cave. In Figure 3, the Strong's Cave marsupial-bearing deposits are shown as younger than those of Mammoth Cave, but the poverty of the evidence for this chronology must be emphasized.

The main fossiliferous deposit in Strong's Cave is in the entrance chamber, in which a talus slope appears to have been undermined by stream action and let down in its central portion, leaving ledges of undisturbed talus against the walls of the cave. The central, undermined portion of the talus slope still receives debris from the surface, and before systematic collection began, was littered with bones. No doubt some of this relatively young bone falls into the stream, but the stream also appears to contain older bone derived from lower parts of the talus through the base of which the stream finds its way. Excavations have been made on one of the ledges of undisturbed talus, but have not yet reached the bottom of this talus.

However, these excavations may be a useful guide as to which specimens found in the stream bed represent geologically older and which younger fossils. Thus, ignoring taxa known

only from the surface litter, but including taxa of unknown stratigraphic derivation found in the stream bed, the older Strong's Cave fauna contains the following marsupial species, each quoted with a representative specimen:—

<i>Dasyurus geoffroyi</i>	65.9.18
Small dasyurids	67.4.72
<i>Sarcophilus harrisi</i>	65.9.8
<i>Thylacinus cynocephalus</i>	65.6.56
<i>Isodon obesulus</i>	66.9.44
<i>Cercartetus concinnus</i>	65.9.33
<i>Trichosurus vulpecula</i>	65.9.9
<i>Potorous gilberti</i>	65.12.444
<i>Petrogale lateralis</i>	66.5.41
<i>Setonix brachyurus</i>	65.9.15
<i>Protemnodon</i> (anak according to Cook 1963a)	61.11.16
<i>Macropus</i> cf. <i>eugenii</i>	65.9.16
<i>Macropus irma</i>	65.6.49
<i>Macropus fuliginosus</i>	65.9.20
<i>Sthenurus occidentalis</i>	61.11.10
<i>Sthenurus browni</i>	65.9.28
<i>Zygomaturus trilobus</i>	61.11.20

The talus slope in the entrance chamber of Strong's Cave has yielded shallowly buried human remains (e.g. A 1511), snail shells in abundance, and other organic remains.

Devil's Lair

This is a small chamber near the entrance to Nannup Cave, about 300 yds east of Strong's Cave; it is the site referred to by Lundelius (1960, 1966) and Cook (1960) as "Nannup Cave". Lundelius (1960) reports radiocarbon dates of $8,500 \pm 160$ years B.P. and $12,175 \pm 275$ years B.P. on charcoal samples from Devil's Lair; the older sample does not represent the bottom of the deposit, which may represent a considerable span of late Pleistocene time. A human incisor tooth (A 16284), portion of a baler shell (Chicago Nat. Hist. Mus. PE 11150) and stone artefacts (not yet traced) were recovered by Lundelius in his excavation in Devil's Lair, but their stratigraphic relationship to the dated charcoal samples is not known (I. M. Crawford, pers. comm.). Lundelius (1960) records *Sarcophilus harrisi* (the Tasmanian Devil) in both his bone samples from Devil's Lair, whence the locality name now in use. An account of the human tooth is in preparation by P. L. Davies (University of Sydney).

Other caves in the Cape Leeuwin-Cape Naturaliste region

Collections made from surface litter in numerous caves (Lowry 1967) in this region suggest that the following marsupial fauna has been characteristic of the region for some hundreds or possibly even a few thousand years prior to European occupation. The representative specimen quoted is usually from Harley's Cave.

<i>Dasyurus geoffroyi</i>	66.2.68
Small dasyurids	65.9.51
<i>Sarcophilus harrisi</i>	65.2.85
<i>Thylacinus cynocephalus</i>	64.1.9
<i>Isodon obesulus</i>	66.2.63
(<i>Perameles</i> , of the <i>bougainville</i> group.	Not
abundant.	66.2.53)
<i>Cercartetus concinnus</i>	64.1.28
<i>Trichosurus vulpecula</i>	65.12.17
<i>Pseudocheirus occidentalis</i>	65.12.294
<i>Potorous gilberti</i>	66.2.43
<i>Bettongia penicillata</i>	65.12.320
(<i>Bettongia lesueuri</i> .	Not abundant.	66.2.97)
<i>Petrogale lateralis</i>	66.1.3
<i>Setonix brachyurus</i> .	Abundant.	66.2.16
<i>Macropus eugenii</i>	65.10.84
<i>Macropus irma</i>	66.2.5
<i>Macropus fuliginosus</i>	66.1.1

Bridgetown

A report quoted at second hand by Woodward (1890) suggests that *Diprotodon* remains were found, probably in gravels being worked for tinstone, near Bridgetown. The specimen has not been traced.

Mather Road Quarry, Fremantle

A section in Mather Road (Deane's) Quarry, about 1 mile south of Fremantle shows a thin (about 1 inch thick) bed densely crowded with lagoonal molluscs at about 1 ft above modern mean sea level, overlain by thin beds of unfossiliferous sand and clay, overlain in turn by cross-bedded aeolianite typical of the "Coastal Limestone". This aeolianite is truncated almost horizontally by a buried soil with a thickness frequently exceeding 3 ft. The thick fossil soil is overlain in turn by at least three consolidated calcareous dunes separated from one another by thin fossil soils. The upper parts of these upper dunes are densely calcareous, and the whole aeolianite sequence is perforated by calcareous "solution pipes" (Fairbridge 1950). Above the aeolianite, and filling the solution pipes, is a red or yellow sandy soil with a plant cover.

The consolidated dune immediately above the thick fossil soil in the southwestern portion of Mather Road Quarry has yielded a mandible and lower part of a skull of a wombat (65.4.61), firmly cemented in tough, compact, "clean", pale-coloured, massive aeolianite. The mandible is displaced backward only about 5 mm. from its natural articulation with the skull. None of the post-cranial skeleton appears to be represented among the additional scraps of bone preserved, and it is not clear whether the upper part of the skull was removed before or after burial, because the piece of rock enclosing the specimen was quarried out and dressed as building stone before the specimen was noticed. I have compared the Mather Road Quarry wombat directly with the Mammoth Cave wombat sample, and they appear to be conspecific, but my studies on wombats are not yet sufficiently advanced for confidence about the degree of relationship of these Western Australian fossil wombats (i.e. *Vombatus hacketti*) with the modern bare-nosed wombats of south-eastern Australia.

Charcoal from the upper parts of the thick fossil soil below the wombat has been dated at $26,800 \pm 1,050$ years B.P. (date no. GaK-875). Thus it would appear that wombats persisted in the Perth metropolitan region into late Pleistocene time.

McIntyre Gully, Gingin

"Pleistocene drift" at McIntyre Gully is described by Feldtmann (1963), and the discovery of nototherian remains in this drift by Main (1949). The specimen concerned (64.10.16) appears to be referable to *Zygomaturus trilobus*.

Wanneroo

I have described (Merrilees 1968a) an occurrence of *Sthenurus browni* with another macropod and possibly also a reptile from a locality not precisely recorded, but in the Wanneroo district near Perth. The specimens may come

from an old cave fill and are likely to be of late Pleistocene age.

Douglas, Kendrick and Merrilees (1966) describe another site in the Wanneroo district which appears to have been the feeding place of *Sarcophilus* (probably *harrisi*), also of late Pleistocene age.

Hastings Cave

Lundelius (1960) describes excavations in a cave in the Jurien Bay area which he calls "Drover's Cave", but the same cave is known as Hastings Cave by the Western Australian Speleological Group and in various Museum records, and is called Hastings Cave by Lundelius (1957) and Ride (1960 p. 76). Lundelius (1960) reports radiocarbon dates of $5,900 \pm 140$ years B.P. and $7,850 \pm 170$ years B.P. for the upper parts of his excavations in Hastings Cave; it is possible that the lower parts extend back into Pleistocene time. Lundelius (1960) gives a faunal list including *Protomnodon anak*; this record is based on a single molar tooth now in the collection of the Chicago Natural History Museum (E. L. Lundelius, pers. comm.).

Wedge's Cave

Lundelius (1960) describes an excavation to a depth of $8\frac{1}{2}$ ft in Wedge's Cave, and a radiocarbon date of $3,750 \pm 240$ years B.P. for a sample from depths between $1\frac{1}{2}$ and $3\frac{1}{2}$ ft. The lowest parts of the deposit may represent late Pleistocene time. See also Lundelius (1966).

Other caves in the Moore River-Dongara region

Surface collections made from many caves in this region presumably represent the fauna for some hundreds of years prior to European occupation, but probably not thousands of years in view of the radiocarbon dates reported by Lundelius (1960) for shallowly-buried deposits in Hastings and Wedge's Caves. Owl pellet deposits are of frequent occurrence, providing samples of the small nocturnal mammals of the region.

The following marsupial taxa (with a representative specimen usually from Weelawadji Cave) are characteristic of surface litter in caves in the Moore River-Dongara region:—

<i>Dasyurus geoffroyi</i>	65.4.1
Small dasyurids	65.4.21
<i>Isodon obesulus</i>	65.3.26
<i>Trichosurus vulpecula</i>	65.12.187
<i>Pseudocheirus occidentalis</i>	65.4.27
<i>Bettongia penicillata</i>	65.4.25
<i>Bettongia lesueuri</i>	65.9.94
<i>Macropus irma</i>	65.4.29
<i>Macropus fuliginosus</i>	65.4.32

In addition, *Thylacinus cynocephalus* (61.2.22) *Perameles* of the *bougainville* group (66.2.109), *Potorous platyops* (65.12.423) and one or more species of small macropodines, not so far identified (e.g. 65.12.193, 194) occur at shallow depths. *Setonix brachyurus* (65.5.2) occurs in surface litter in caves in the Yanchep district, south of the region under discussion, but within the Moore River-Dongara region *Setonix* is recorded only from the lower parts of the Hastings Cave deposit (Lundelius 1960). *Sarcophilus* is reported at shallow depth by Lundelius (1960, 1966).

"Balladonia"

The occurrences described by Glauert (1912b), Fairbridge (1953) and others under "Balladonia" actually refer to a number of localities in the Balladonia district, the most richly fossiliferous of these localities being Wonberna, about 12 miles south south west of Balladonia homestead. It is difficult now to reconstruct the original stratigraphy at any of the Balladonia complex of deposits, but in most cases (except perhaps Guralia, about 17 miles west of Balladonia homestead) there appears to have been at least one bone-bearing clay member and a thin (under 2 ft thick) paraconglomerate (Pettijohn 1957) made up of rounded pebbles of crystalline and other rocks, angular rock fragments, bone (some rolled, but most of it unworn, though fragmented) and finely divided material, all firmly united by calcareous cement. This paraconglomerate appears to represent a brief depositional episode which incorporated bone (much of it fragmented, probably by carnivores), rock fragments of varying sizes, pebbles relict from an earlier erosional cycle, and finely divided mineral material into a single thin bed, then or later infiltrated by calcareous solutions. It is possible that such an episode interrupted accumulation of clay deposits only once, simultaneously in several parts of the Balladonia district, with the corollary that all the bone-bearing deposits are approximately contemporaneous.

I have found worked stone implements (A 16357 and A 16358) in the paraconglomerate at Wonberna. Marsupials so far identified from the Wonberna paraconglomerate include:—

<i>Sarcophilus cf. harrisi</i>	67.6.10
<i>Thylacoleo</i> , probably not <i>carnifex</i>	66.11.21
Small potoroine, possibly <i>Caloprymnus campestris</i>	66.6.44
Small macropodine, possibly <i>Onychogalea lunata</i>	66.7.5
<i>Phascolonius cf. gigas</i>	67.1.144
<i>Lasiorhinus latifrons</i>	67.1.45

The Wonberna paraconglomerate contains fragments of bones large enough to represent *Diprotodon* though diagnostic specimens are lacking. *Diprotodon* certainly occurred at Wonberna (65.2.80), but possibly in clay.

Stone artefacts (A 14929, A 14934) have been found also in coarse bone-bearing sandstone at Guralia, and it is possible that other kinds of deposits in the Balladonia district are approximately contemporaneous with human occupation of the district. If so, several species of *Sthenurus*, not so far specifically identified, must also be listed as contemporaneous with man. The probable specimens upon which Glauert (1912b) based his report of *Protemnodon anak* from the Balladonia district appear to me to be referable to *Sthenurus*, and I have not been able to trace the specimen(s) upon which Glauert based his record of *Macropus magister*.

Dark patches on bone from the Balladonia district (e.g. 67.8.78-99) might represent charring, or might represent mineral staining.

Caves in the southern portion of the Nullarbor region

Numerous caves occur (Jennings 1961, 1963) in the southern part of the Nullarbor region, and surface litter within these caves has yielded the following marsupial fauna. Most of the representative specimens listed are from Thylacine Hole (N 63)—see Lowry and Lowry (1967). See also Cook (1963b) and Lundelius (1957, 1963, 1966).

<i>Dasyurus geoffroyi</i>	Geol. Surv. West. Aust. F 6302
Small dasyurids	67.4.379, 67.4.381
<i>Sarcophilus harrisi</i>	Geol. Surv. West. Aust. F 6328
<i>Thylacinus cynocephalus</i>	" " " " F 6357
<i>Macrotis lagotis</i>	" " " " F 6333
(<i>Isodon obesulus</i> , Not abundant.	67.8.65)
<i>Perameles</i> , cf the <i>bougainville</i> group.	Abundant.
	Geol. Surv. West. Aust. F 6321
<i>Chaeropus ecaudatus</i>	67.4.334
<i>Trichosurus vulpecula</i>	Geol. Surv. West. Aust. F 6345
<i>Caloprymnus campestris</i>	67.3.22
<i>Bettongia cf. penicillata</i>	67.3.98
<i>Bettongia cf. lesueuri</i>	67.3.97
<i>Onychogalea lunata</i>	67.4.291
<i>Lagorchestes hirsutus</i>	67.3.34
<i>Lagostrophus fasciatus</i>	66.12.14
Large macropodine, probably <i>Megaleia rufa</i>	Geol. Surv. West. Aust. F 6301
<i>Lasiorhinus latifrons</i>	" " " " F 6314

Pseudocheirus is known from a single specimen (67.4.374) in the Western Australian Museum collection and from a report by Lundelius (1963). *Potorous platyops* and *Cercartetus concinnus* are reported by Lundelius (1963) but are not represented in the Western Australian Museum collection and a single specimen (67.10.326) appears to represent *Petrogale*.

Desiccated soft tissue from a thylacine (64.8.1) from Murra-el-elevyn Cave has been estimated as $3,280 \pm 90$ years B.P. in age (Partidge 1967, date no. GaK—693). Similar tissue from a thylacine and from a dog in Thylacine Hole (Lowry and Lowry 1967) has been submitted for radiocarbon dating, but results are not yet available; both animals were in about the same state of preservation, far more complete than the Murra-el-elevyn thylacine, and hence presumably younger.

Little excavation has been undertaken in caves in the Eucla Division, but Lundelius (1963) reports the occurrence of a single lower permanent premolar tooth of *Sthenurus* (probably *S. gilli*—see Merrilees 1965) at shallow depth in Madura Cave. Madura Cave is described by Frost (1958). Some excavation has been conducted by D. C. and J. Lowry in Cocklebidly Cave, revealing the presence there of *Sarcophilus* and other marsupials, but detailed study of the material excavated has not yet been made.

Dingo Rock, Karonie

Specimens 3650a, b and c, and probably also 66.8.25 and 66.8.26, represent *Diprotodon* (of indeterminate species) from this locality.

Lake Darlôt

A very worn, edentulous mandible (64.10.17) from about 40 miles west of Lake Darlôt probably represents a species of *Diprotodon*. (See Woodward 1909.)

Great Victoria Desert

Passing reference is made by Glauert (1912b, p. 50) to a fragment of bone attributed to a species of *Diprotodon* found in the Great Victoria Desert by the Elder Exploring Expedition in 1892. The specimen has not been traced.

Oakover River

The edentulous palatal region of a very large skull (Univ. West. Aust. Geol. Dept. specimen 50181) from the Oakover River near Old Braeside homestead probably represents a species of *Diprotodon*, but may differ from the Lake Callabonna species.

Billabalong and related sites on the middle Murchison River

A well preserved nototherian mandible (61.2.1) was found in a dry bed of the Murchison River near the road crossing on Billabalong Station by H. White about 1957, and other bone fragments have been found nearby on subsequent occasions. The Billabalong, Gingin, Mammoth Cave and Strong's Cave nototherians all appear to be referable to *Zygomaturus trilobus*.

The Billabalong specimen was found in a formation known informally as the "Murchison cement", which occurs along the middle reaches of the Murchison River as a very coarse sandstone, with lenses of conglomerate. At Coolarburloo Pool, about 10 miles downstream from the notothere locality, I found a worked stone implement (A 15000) in situ in the "Murchison cement", and further downstream still, about 2 miles southeast of Yallalong homestead, a tektite (G 12114) apparently in situ in a conglomerate lens.

The "Murchison cement" appears to be a very widespread formation, and has yielded at least one other artefact (A 13664, from Maralya Mill, Muralgarra Station), fossil plants from various localities (e.g. P 66.37 from Yallalong Station), and fossil land and aquatic snails of several kinds, including *Coxiella* from the Ederga River (62.132-135 etc.), *Austrosuccinea* from Thundelarra Station (61.285), *Sinumelon* (e.g. 61.283-284) from several localities, and a fragmentary specimen (61.281) from the Ederga River which may represent (G. W. Kendrick, pers. comm.) a rhagadid snail. If 61.281 is indeed a rhagadid, it would represent the most southerly known occurrence for this family, which at present is known only northwards from Shark Bay. A single vertebra (G 11915), found by A. R. Main in the west bank of the Ederga (Salt) River on Barnong Station near a watering point known locally as Mooloo Well, may be crocodilian. A reptilian, possibly varanid, tooth (G 4486) from a well near the junction of Aurillia Creek with the Gascoyne River, may also represent the "Murchison cement".

The tektite (G 12114) mentioned above was exposed at a more or less horizontal erosion surface in what appeared to be a conglomerate lens in the "Murchison cement". It could not be detached from this surface by finger pressure alone, but came away readily when the rock surface about 1 cm. away was subjected to blows from a hammer while finger pressure was applied to the tektite; there is little doubt that

this tektite formed a "pebble" in the conglomerate. This tektite may have fallen into the conglomerate while the latter was being accumulated, but probably it was reworked from some older surface into the conglomerate. It is widely believed that the whole australite "strewn-field" represents a single fall (e.g. Chapman in O'Keefe 1963), but there is uncertainty about the time of this fall. Rubidium-strontium (Pinson and Schnetzler 1961) and potassium-argon (Zähringer in O'Keefe 1963) isotope ratio dates and geomagnetic reversal dates (Glass & Heezen 1967) suggest an age of formation for the australites (and perhaps of all the other "Far Eastern" tektites) of about 600,000-700,000 years B.P. On the other hand, geological field evidence so far reported suggests a much more recent time of fall (Fenner 1935, Baker 1959, Barnes in O'Keefe 1963, Johnson 1965, Gill 1965). Dury (1966a, entry no. 170) reports a date of 7,380 years B.P. as a "possible maximum" for the time of fall of australites in southern Victoria. In view of current uncertainty about the nature of tektites (see reviews by O'Keefe and by Cohen in O'Keefe 1963), it remains an open question whether the time of formation of the australites has any close relationship to their time of fall on Australia. It is reasonable to postulate that the time of formation of the conglomerate lens near Yallalong homestead, and therefore probably of the whole "Murchison cement" must be late Quaternary, and may be Recent.

There is a report (Mrs A. E. Crocker, pers. comm.) of an australite having been found in paraconglomerate in a dam excavation at North Rocks in the Balladonia district. The specimen has not been traced. No fossils have been reported from North Rocks, but the paraconglomerate there resembles its fossiliferous counterpart at Wonberna, and may be of the same age.

The artefacts in the "Murchison cement" show that its formation post-dated human occupation of the Coolarburloo Pool-Muralgarra district. The Ederga River crocodilian vertebra may have been reworked from some pre-existing deposit into the "Murchison cement", but the Billabalong *Zygomaturus* mandible is far too complete and too well preserved to be reworked. I conclude that *Zygomaturus trilobus* and man were contemporaries in this district.

Caves on North West Cape

Several expeditions have investigated these caves, and fossil marsupials have been collected from them. No extinct species have been recognized in these collections. The pelvis of a dog (presumably a dingo—67.7.2) has been recovered from a consolidated "cave earth" in a cave without formal name, recorded as "WAM Cave 6" in Western Australian Museum records.

Quanbun

Glauert (1921a) reports the finding of marsupial and crocodile remains in an excavation on Quanbun Station. The site is about 7 miles north of Quanbun homestead and was

formerly called "Alligator Dam" but is now known locally as "Jubilee Dam". The specimens upon which Glauert (1921a) based his identifications were not numbered, and are not now recognizable with certainty. However it is probable that the specimens now catalogued as 65.2.33—35 and others represent *Phascodon gigas* from Quanbun, 63.11.8 and 67.7.9 a large macropodine resembling *Protemnodon anak*, 61.7.9 another large macropodine, and 66.8.23—24 and G 3637 a crocodilian.

Cherrabun

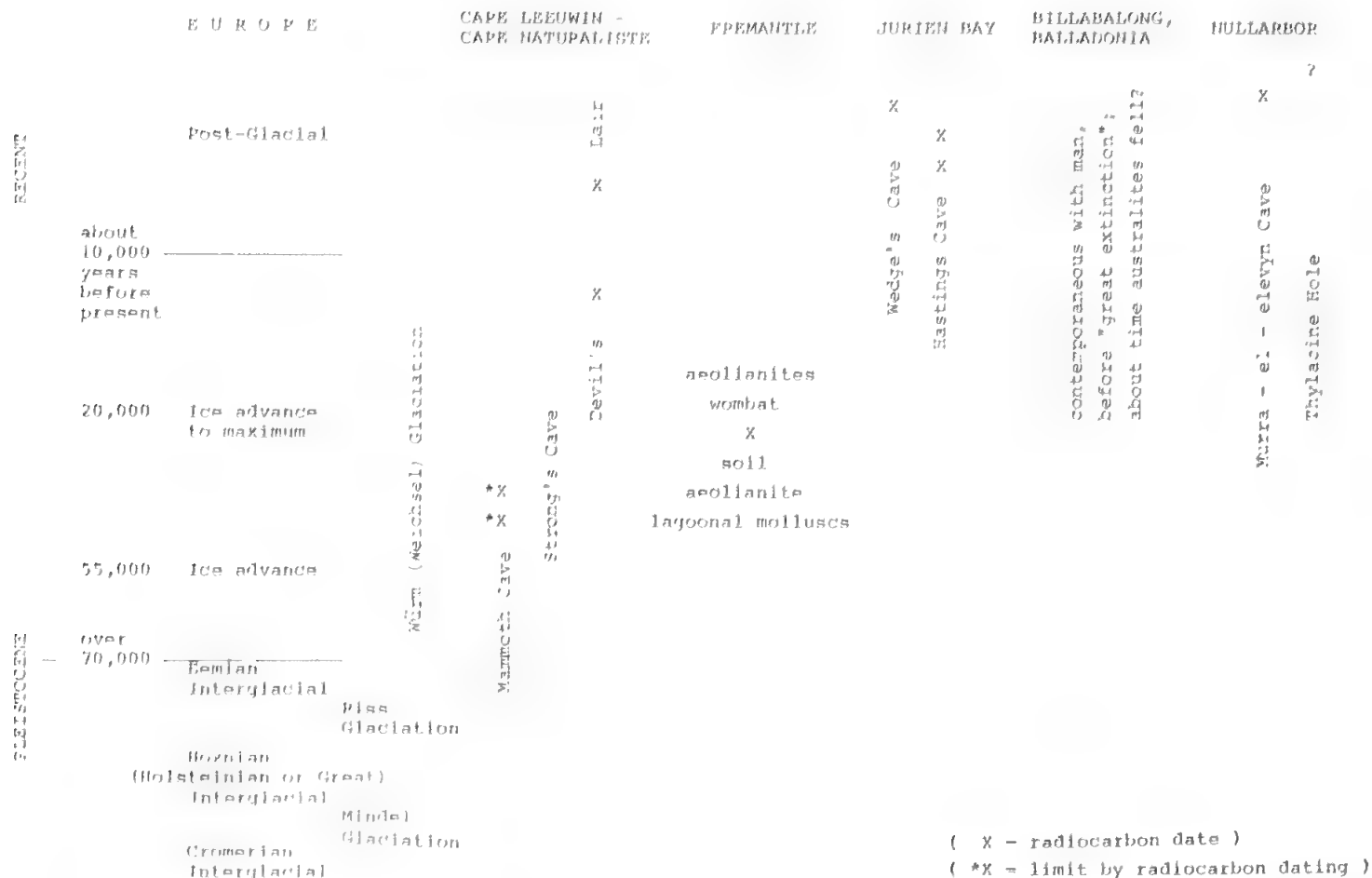
There is an unpublished record in the Western Australian Museum geological catalogues

of the occurrence of a large macropodine (possibly the specimens now catalogued as 61.7.10—11) and a crocodilian (G 3529 a — d) in a well at the "foot of St. George Range, Cherrabun Station, Fitzroy River".

Windjana Gorge

The earliest report of fossil marsupials in Western Australia is that of Hardman (1884). His specimen is not now traceable, but it appears to have been the head of a *Diprotodon* femur found near the western (downstream) entrance to Windjana Gorge (Hardman 1887). Recent searches by myself and others have failed to find additional specimens.

FIG 3 LATER QUATERNARY TIME.



Discussion and conclusions

Man and the larger marsupials on the Australian mainland

It is shown above that the following larger marsupials were present with man on the Australian mainland in late Quaternary time, only to become extinct there before historic time:—

Sarcophilus—at Devil's Lair, "Balladonia", Lake Menindee, Lake Tandou, Devon Downs, Fromm's Landing, Korolt Beach, Bushfield, possibly other sites on the basalt plains of western Victoria, Padyadiy. All specimens probably conspecific.

Thylacynus—at Lake Menindee, Lake Tandou, Devon Downs, Fromm's Landing, Lake Colongulac. All specimens probably conspecific.

Thylacoleo—at "Balladonia", Lake Menindee, Lake Colongulac. Probably more than one species represented.

Propleopus—one species at Lake Menindee.

Macropus—at Lake Menindee, Lake Tandou, Lake Colongulac, Pejark Marsh. Several species involved.

Protemnodon—at Lake Menindee, Lake Tandou, and possibly one or more sites on the basalt plains of western Victoria. Possibly more than one species involved.

Sthenurus—at Lake Menindee and probably at "Balladonia". Several species involved.

Procoptodon—at Lake Menindee, Lake Tandou, Lake Colongulac. All specimens probably conspecific.

Diprotodon—at Lake Menindee, Lake Colongulac, Pejark Marsh and possibly at "Bal-

ladonia", Port Augusta, Lake Tandou and Forbes. Possibly more than one species involved.

Palorchestes—at Pejark Marsh. Probably only one species.

Zygomaturus—at Billabalong. Only one species involved.

Large wombats—*Phascolonus* at "Balladonia" and probably also Lake Tandou; probably only one species. Another species of large wombat at Lake Menindee.

It is known that some taxa now extinct survived until very late Quaternary time. Thus, Grant-Taylor and Rafter (1963) record a radiocarbon date (NZ-206, listed by Dury 1964) of $6,700 \pm 250$ years B.P. on dentine from mandibular teeth of a species of *Diprotodon*, from Orroroo, eastern South Australia. The specimen apparently was not directly associated with evidence of the presence of man. Tedford (1967 p. 149) considers this date to be at variance with field evidence, but he accepts a date (NZ-381) of $11,100 \pm 130$ years B.P. (Grant-Taylor and Rafter 1963) on another specimen of *Diprotodon*, also from the Orroroo district, and suggests it might apply also to *Sthenurus* in this district. *Protemnodon anak* is reported by Lundelius (1960) to have survived into Recent time in the vicinity of Hasting's Cave Jurien Bay, Western Australia. Thus at least two species of large herbivores, now extinct, survived into very late Quaternary time. *Sarcophilus* (Gill 1955c) and *Thylacinus* (Partridge 1967) survived into Recent time on the Australian mainland; both genera survived the "Great Australian Arid Period", *Sarcophilus* persisting almost to historic time.

On the other hand, Mulvaney (1964a), Mulvaney and Joyce (1965), Hossfeld (in Cotton 1966), Mulvaney (1966a) and Macintosh (1967) show that man had arrived in Australia before the end of Pleistocene time. Dury (1966a, entry no. 274) lists a date of $22,700 \pm 700$ years B.P. (GaK-629), said to require confirmation, for human occupation at Malangangerr, Northern Territory. The earlier date ($26,300 \pm 1,500$ years B.P.) listed by Tedford (1967) for Lake Menindee applies to the upper parts of the B horizon in the soil profile, and it is suggested that accumulation of the parent material of the soil may have been slow; human occupation below this upper level is reported, and appears to indicate human occupation of the Lake Menindee region much earlier. I have found mussel shell, presumably transported by humans, near the bottom of the B horizon at Lake Tandou; if the fossiliferous deposit at Lake Tandou represents the same depositional episode as that at Lake Menindee, there is evidence of similarly early human occupation. Gallus (1966) estimates from the depth of an artefact-bearing deposit in Koonalda Cave, Nullarbor region, South Australia, a date earlier than 30,000 years B.P. for human occupation of this area.

Some of the bone excavated by Glauert from the Mammoth Cave deposit is charred (e.g. 67.6.11-21) and this charring conceivably could result from deliberate cooking of game animals by man. However, there appears to be no other evidence of human occupation of the area, and

the site itself does not appear a likely one for human occupation, since it is now dark (but see Rosenfeld 1964), and may have been even further from the entrance and thus no less dark at the time of accumulation. Apparently there was much charcoal disseminated through the deposit (shown by Geol. Surv. West. Aust. specimen 10089), which presumably fell through holes in the cave roof along with other debris from outside. Both charcoal and charred bone may represent natural bush fires rather than human hearths.

Characteristics of the extinction of larger marsupials in the Cape Leeuwin-Cape Cape Naturaliste region, Western Australia

In this region marsupial-bearing deposits are known which appear to represent a succession in late Quaternary time (see Fig. 3). The Mammoth Cave deposit appears to have been the oldest in this region; specimens obtained by excavation in Strong's Cave and Devil's Lair are probably younger; the surface litter of bones in many caves in the region is probably younger still, and there are some records of the fauna in historic time (e.g. Glauert 1933, 1950), including museum specimens.

The Mammoth Cave deposit has yielded 21 species of larger marsupials (see above). Of these 9 species are believed to have lived in the region in historic time (*Dasyurus geoffroyi*, *Isodon obesulus*, *Trichosurus vulpecula*, *Pseudochirus occidentalis*, *Potorous gilberti*, *Macropus eugenii*, *M. irma*, *M. fuliginosus*, *Setonix brachyurus*). 6 species (one each of *Sarcophilus*, *Thylacinus*, *Perameles*, *Phascolarctos* and *Vombatus*, and a wallaby resembling *W. bicolor*) are either identical with or closely related to species still surviving in other parts of Australia. 6 species (one each of *Thylacoleo*, *Protemnodon*, *Zygomaturus*, two of *Sthenurus*, and a large macropodine resembling but not conspecific with *M. fuliginosus*) appear to be extinct everywhere.

Three species which appear to have lived in the Cape Leeuwin-Cape Naturaliste region in historic time are not known from the Mammoth Cave fossil deposit, viz. *Bettongia penicillata*, *B. lesueuri* and *Petrogale lateralis*; these may represent invasion of the area in a time subsequent to accumulation of the Mammoth Cave deposit.

Excavations in Strong's Cave and Devil's Lair have yielded one species each of *Sarcophilus*, *Thylacinus*, *Perameles*, *Protemnodon* and *Zygomaturus* and two species of *Sthenurus*, but none of *Thylacoleo*, *Phascolarctos* or *Vombatus* nor the macropodines resembling *Macropus fuliginosus* or *Wallabia bicolor*. However, *Vombatus* persisted in the Fremantle district after 26,800 years B.P., and its absence from Strong's Cave and Devil's Lair may be due to accidents of preservation. Specimens of *Phascolarctos* collected by L. Glauert from Bride's Cave (e.g. 64.2.23) may be from surface litter; if so, absence of *Phascolarctos* from Strong's Cave and Devil's Lair may also be an accident of preservation. Equally, other absences from the Strong's Cave and Devil's Lair faunal list may be due to accidents of preservation, but it is reasonable to suggest that the much shorter list of large extinct marsupials in Strong's Cave

plus Devil's Lair than in Mammoth Cave may be due to some of the taxa concerned having become extinct in a period of time elapsed between accumulation of the respective deposits.

I have shown (Merrilees 1968a) that more individuals of *Sthenurus occidentalis* are represented in the Mammoth Cave deposit than of *S. brownei*, but that there are more individuals of *S. brownei* than of *S. occidentalis* in the smaller sample of *Sthenurus* from Strong's Cave. It is known Merrilees (1968a) that *S. brownei* survived in the Wanneroo district until very late Quaternary time. Thus it is likely that *S. brownei* survived in the Cape Leeuwin-Cape Naturaliste region longer than did *S. occidentalis*, but that both species became extinct in the time elapsed between accumulation of the Strong's Cave deposits and surface litter in other caves in the region.

I have shown also (Merrilees 1968b) that *Perameles* was more abundant than *Isoodon* at the time of accumulation of the Mammoth Cave deposit, but much less so at later times, declining to extinction before historic time.

Thylacinus and perhaps *Phascolarctos* are represented in surface litter in caves in the region and probably persisted into Recent time before becoming extinct, while *Sarcophilus* and *Petrogale lateralis* are known to have persisted into Recent time before becoming extinct, since they are recorded for the upper parts of an excavation in Devil's Lair by Lundelius (1960) as well as occurring in surface litter in other caves.

Thus it would appear that late Quaternary time in the Cape Leeuwin-Cape Naturaliste region is characterized by the following changes among the larger marsupials:—

1. Extinction without replacement by related species.
2. Gradual species by species impoverishment, not sudden mass extinction.
3. Migration into the area very limited.

In no other part of Western Australia is information available, particularly from older deposits, in sufficient detail to give much insight into marsupial history. However, in the Balladonia region, some of the species (of *Lasiacanthus*, *Onychogalea*, and possibly *Caloprymnus*) represented in the fossiliferous deposits survived into historic time. The fossil *Sarcophilus* species may be the same as that still surviving in Tasmania. Several fossil species of *Sthenurus*, and one each of *Diprotodon*, *Thylacoleo* and *Phascolonus*, appear to be totally extinct. Further east, deposits in the caves of the southern Nullarbor region suggest a similarly partial extinction. Desiccated carcasses of *Trichosurus*, *Dasyurus*, *Sarcophilus* and *Thylacinus* of relatively fresh appearance, found alongside similarly preserved remains of *Lasiacanthus* and *Canis* in Thylacine Hole (Lowry and Lowry 1967) suggest that species have disappeared one by one from this region, that even Bassian species survived the "Great Australian Arid Period" in the region, and that some such species may still survive there. On the other hand, some apparently Bassian species such as *Sthenurus gilli* (Merrilees

1965) appear to have disappeared earlier from the southern Nullarbor region.

Survival rate of Western Australian marsupials

Australia is large enough to come under very different climatic controls in different regions at any given time (Gentilli 1949, 1961). It is often regarded as having three major zoogeographic divisions, Torresian, Eyrean and Bassian. See Keast (in Keast, Crocker and Christian 1959) for an account of these divisions and various subdivisions. Western Australia also is large enough for all three major zoogeographic provinces to be represented, the Torresian in the Kimberley Division, the Bassian in the South West and western part of the Eucla Divisions and Eyrean elsewhere.

Fossil deposits occur in each of the three modern zoogeographic regions, e.g. Mammoth Cave within the Bassian, "Balladonia" and Billabalong in the Eyrean, Quanbun in the Torresian region. Thus it is not unreasonable to compare the whole known fossil fauna of larger marsupials with the whole known modern fauna in what at first appears to be an arbitrary political entity, namely the state of Western Australia.

Considering only marsupials of about the size of a rabbit or larger, I estimate that 17 species, known from Western Australian fossil deposits, became extinct in Western Australia before historic time, and that 34 species live in Western Australia at the present time. The extinct and the surviving species in Western Australia are listed below, and these lists are the basis of the Western Australian entry in Figure 1.

Larger marsupials extinct in Western Australia before historic time—

1. *Sarcophilus harrisi*
2. *Thylacinus cynocephalus*
3. *Phascolarctos* cf. *cinereus*
4. *Thylacoleo* sp., not *carnifex*
5. *Vombatus hacketti*
6. *Phascolonus gigas*
7. *Sthenurus occidentalis*
8. *Sthenurus brownei*
9. *Sthenurus* sp. ("Balladonia")
10. *Sthenurus* sp. ("Balladonia")
11. *Sthenurus* cf. *gilli*
12. *Protemnodon* sp., possibly *brehus*
13. Wallaby resembling *W. bicolor*
14. *Macropus* sp. (Mammoth Cave)
15. *Zygomaturus trilobus*
16. *Diprotodon optatum*
17. *Diprotodon* sp. (Oakover River)

(17 species counting the Oakover River species of *Diprotodon* as distinct from that at Balladonia, Karonie etc., and counting 3 species of *Sthenurus*, including one resembling *gilli*, for the Balladonia complex of sites.)

Larger marsupials persisting in Western Australia into historic time—

1. *Dasyurus geoffroyi*
2. *Dasyurus hallucatus*
3. *Perameles bougainville*
4. *Isoodon obesulus*
5. *Isoodon barrowensis*
6. *Isoodon macrourus*
7. *Macrotis lagotis*
8. *Chaeropus ecaudatus*

9. *Wyulda squamicaudata*
10. *Trichosurus vulpecula*
11. *Pseudocheirus occidentalis*
12. *Pseudocheirus dahli*
13. *Lasiorninus latifrons*
14. *Macropus fuliginosus*
15. *Macropus robustus*
16. *Macropus antilopinus*
17. *Macropus agilis*
18. *Macropus irma*
19. *Macropus eugenii*
20. *Setonix brachyurus*
21. *Megaleia rufa*
22. *Lagorchestes conspicillatus*
23. *Lagorchestes hirsutus*
24. *Lagostrophus fasciatus*
25. *Onychogalea unguifer*
26. *Onychogalea lunata*
27. *Petrogale lateralis*
28. *Petrogale rothschildi*
29. *Peradorcas concinna*
30. *Potorous gilberti*
31. *Potorous platyops*
32. *Bettongia lesueuri*
33. *Bettongia penicillata*
34. *Caloprymnus campestris*

(34 species, counting *Caloprymnus campestris*, although this species is not adequately documented for Western Australia so far.)

Several assumptions are implicit in Figure 1. One is that all the species of large marsupials at present living in Western Australia were here in late Pleistocene time, and are not recent immigrants; in fact, not all the modern species listed above are known from late Pleistocene fossiliferous deposits. Of the modern species which are also known as fossils, not all of them now live in the areas they once inhabited. Also, it is probable that as additional fossiliferous deposits become known, marsupial species hitherto unrecorded will become known. It is even possible that additional modern species remain to be discovered. However, taking the lists of surviving and extinct taxa at their face value, as Martin (1966) appears to do in his calculations, the Western Australian rate of survival of larger marsupial species from late Pleistocene time is

$$\frac{34}{34 + 17} = 67\%$$

There is no justification at present for assuming a sudden disappearance of the extinct 33% of species, and this assumption has not been made in Figure 1.

It is known that man appeared, probably in late Pleistocene time during the lifetime of several species now extinct, and it is often claimed that a disastrously arid climatic episode (see above) occurred in Recent time. These factors are also shown in Figure 1.

The South West Division of Western Australia is uniformly Bassian in the zoogeographic sense, and since not only its modern but also its fossil fauna is slightly better known than that of any other part of the state, it is instructive to consider this Division separately from the survival point of view.

Of the extinct species listed above, nos 1-5, 7, 8, and 12-15 (11 species) are recorded from the

South West Division. The modern fauna of larger marsupials in this Division includes nos 1, 3, 4, 7, 10, 11, 14, 18-20, 27, 30-33 (15 species) from the modern list above. Thus the survival rate

$$\frac{15}{11 + 15} = 58\%$$

for this Division does not differ greatly from that for the whole state (67%) shown in Figure 1.

Predation by man and dog

Not only did Aborigines hunt marsupials but also they are reported (Meggitt 1965) to have employed semi-domesticated dogs (dingoes) in hunting, and to have followed wild dingoes on the trail of prey in order to take the prey for themselves. Meggitt (1965) suggests that neither practice was in general very successful, and that Aborigines kept dingoes primarily as pets, watchdogs and possibly bed-warmers rather than as hunters.

It is generally believed (Jones 1921, 1925) that Aborigines introduced the dingo into Australia, probably in Recent time because the dingo does not appear to have reached Flinders Island or Tasmania (Tindale in Keast, Crocker and Christian 1959, Macintosh 1967) as it probably would have done if it had been present during the glaciation which joined these areas to the emergent mainland (Browne 1945). If trading contacts between Indonesia and Australia extend back further than suggested by Mulvaney (1966b) for Macassan trepang fishermen, it is possible that dogs were traded, and not necessarily associated with a wave of Aboriginal invaders as often assumed (e.g. Hossfeld in Cotton 1966, cf. Birdsell 1967). Macintosh (in Appendix 2, Mulvaney, Lawton and Twidale 1964) states that the Fromm's Landing dingo (see above) which is about 3,000 years old, is the "oldest genuinely dated dingo" in Australia. Campbell, Edwards and Hossfeld (in preparation) show that dingoes were present in South Australia much earlier in the Recent. (Edwards, pers. comm).

The dog tooth allegedly from the Mammoth Cave deposit (see above) may be mislabelled, and pelvic specimen 67.7.2 from North West Cape (see above), though in a consolidated "cave earth", may not be older than Recent.

Thus the dingo may be a relatively late arrival in Australia, and whether it is wild, feral or partly domesticated, its effects on marsupial species may be difficult to distinguish from those of Recent climatic changes. The presence of dingo and thylacine remains in about the same state of preservation in Thylacine Hole (Lowry and Lowry 1967) suggest that these two species can co-exist in a given area, and this in turn suggests that their effects on marsupial herbivores are not catastrophic.

Predators appear usually to take only part of the populations preyed upon (e.g. Dunnet 1957, Schaller 1966), and even modern man may take heavy toll of various species without destroying them (Marlow 1958, Green 1967) though commercial activities can be very damaging to natural populations (Marshall 1966, C.S.I.R.O. 1964). There appears to be general

agreement that destruction or modification of habitat (e.g. Marlow 1958, Calaby 1966), often by progressive fragmentation of range (Smith in Wright and Frey 1965), is the main process at present leading to extinction of species. Thus it appears safest to seek clues to past marsupial extinctions in habitat modification rather than predation.

Conclusions

The late Quaternary extinction of Australian marsupials may be part of large scale, world wide processes such as the climatic changes linked with waning of the large high latitude ice sheets, and these processes in turn may be of cosmic origin (Steiner 1967.) Behavioural, physiological, ecological or other factors (Gill 1955a), even changes in "will to live" (Tolmachoff 1929), not easily inferred from bony remains and other geological evidence, may be involved. But so far as existing Australian evidence goes, the main alternative hypotheses appear to be mid-Recent aridity and man-made fires.

Additional information of several kinds is needed to decide between these alternatives. Insight into the ecological requirements of living populations of marsupials is needed, as a guide to those of extinct populations. Late Quaternary fossiliferous deposits, adequately dated and representing long time sequences, are needed in climatically disparate localities. Evaluation of early Quaternary or Tertiary marsupial extinctions is needed to decide how distinctive was that of the late Quaternary. But it may be claimed that the hypothesis here advanced of late Quaternary marsupial extinction through habitat modification by man-made fires (a) can be tested (b) is already sufficiently well supported to be worth testing and (c) is likely to prove fruitful under test.

Intensified studies of archaeological sequences in Australia are likely to produce radiocarbon dates on the survival of marsupial game animals, and these are likely to span the last 30,000 years or more. Whether considerable numbers of marsupial species disappeared earlier than, say, 20,000 years ago, and other species have continued to disappear up to historic time, or whether there was faunal stability up to about 6,000 years ago, followed by numerous extinctions in the period 6,000 to 4,000 years ago, should become clear. The same archaeological studies, as well as studies of soils, landforms, plant successions etc., should reveal the occurrences and dates of aridities other than the mid-Recent, or other climatic episodes adverse to mammals.

If man arrived in Australia with "peripatetic pyromania" as part of his cultural tradition, his arrival may be marked in archaeological deposits by sudden increase in abundance of charcoal. If his arrival was followed by rapid decline to extinction of many marsupial species, especially of the larger, more easily hunted kinds, this may be revealed directly in archaeological deposits or marked by a trend away from skinning knives, scrapers and other devices for dealing with large game animals towards millstones or other devices for dealing with plant food and small game, or even possibly by decline in human population. There might be

clues to Aboriginal religious, magical or other practices in a fuller understanding of the marsupial environment in which they were generated, or conversely, clues to marsupial history in Aboriginal oral traditions.

Again, if there was widespread modification of fire-vulnerable marsupial habitats in late Quaternary time, there may have been movement of marsupial species from less fire-vulnerable habitats into niches left vacant by climatic change. Thus disharmonies may be detectable between the physiological capabilities of many modern species, and the demands made upon them in practice in parts of their ranges. It is possible that Australian plant ecosystems have been modified by prehistoric but geologically recent fires on a scale not fully appreciated (Meggitt in Symposium 1960), and that deflected successions may be more common, and climatic climaxes more difficult to identify, than generally thought at present.

Aboriginal man may or may not have had some concept of himself as part of a larger biological system in which nothing he did was without its biological repercussions, and he may or may not have had some awareness of conservation measures (Meggitt 1964, 1965—see also Tolmachoff 1929). If he used fire indiscriminately and expected that its repercussions would not be excessive, he may have been much mistaken, and may have been punished in that most decisive way, by diminution of his food supply and decline in his own numbers, as many other peoples have been punished (Cooke 1931, Meggers and Evans 1957, Fosberg in Symposium 1960, etc.). European man in Australia is no less part of a larger biological system and he too may be punished for any neglect of this fact. His attacks upon the complexity of this biological system, though they may involve less expenditure of energy than Aboriginal firing of large areas of bush, are more insistent, more varied and more studied, and they result in more profound changes. European man may have dispossessed Aboriginal man of a biological system already much impoverished, and he appears bent on continuing this impoverishment for narrow "economic" ends. But impoverished ecosystems are likely to prove unstable (Moore 1967), and we ignore the lessons of conservation (Jennings 1965) at even more peril than the pyromaniac Aboriginal ignored or failed to conceive his.

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2.—Diet of Kangaroos (*Megaleia rufa* and *Macropus robustus*) and merino sheep near Port Hedland, Western Australia

by G. M. Storr*

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Abstract

The diet of kangaroos and sheep grazing freely in the same area on Mundabullangana Station was ascertained in four seasons in 1961. Seasonal variation was studied in the nitrogen and water content of food plants and thus also of the three diets. Estimates were obtained in 1962 of the daily consumption of dry matter by kangaroos. Observations were made on the habitat preferences of the two kangaroos and on their seasonal movements and weight changes.

Introduction

The Pilbara region of the northwest of Western Australia was formerly a large producer of wool. Since the mid-1930s sheep numbers have declined and several stations have been abandoned. Ealey and Suijndorp (1959) attribute this decline to misguided stocking policies and the consequent deterioration of pastures. The pastoralists, however, generally blame the kangaroos, whose numbers are said to have increased enormously since the leases were first taken up.

Little was known of the diet of the kangaroos and sheep, and the writer was directed to make a survey, using the methods developed for Rottnest Island quokkas (Storr 1964). Midna Paddock on Mundabullangana Station (between Port Hedland and Roebourne) was chosen for study. Both the marloo (*Megaleia rufa*) and euro (*Macropus robustus*) were plentiful in the area, and the writer was assured that the paddock would be stocked with sheep throughout the period of study (1961-62).

Environment

Physiography and climate

The study area (see map, Fig.1) is situated 6-10 miles from the sea at an elevation of

20-80 feet. The land rises imperceptibly as one goes inland, and the prevailing flatness of the country is broken only by minor dissection in the vicinity of the Little Yule River and by slightly higher areas that can seldom be called dunes. The soils are mostly sandy to clayey loams, usually of no great depth over impervious clay, which is frequently exposed in wind-eroded areas to form claypans. The Little Yule is a distributary of the Yule River and only flows when the latter is in flood; otherwise it contains no water apart from a few small pools. The claypans retain water for some weeks after heavy rain. During the remainder of the year the kangaroos are as dependent as the sheep on the water in mill troughs.

The climate is characterised by aridity and great summer heat. The mean annual rainfall is 13.6 inches, most of it coming in late summer when cyclonic storms sweep inland from the north. Convectional rain is less frequent here than in the hilly interior of the Pilbara region; hence the relative dryness of December and January. A little rain may reach the area from the south in winter. The period October to December is usually one of unrelieved drought and heat. In Table 1 climatic data (C'wealth Bureau of Meteorology, 1956) are given for Roebourne (80 miles to the WSW) rather than for Port Hedland (40 miles to the ENE)—Roebourne's similar distance from the sea makes it more representative of the study area, for relative humidity decreases and temperature increases rapidly as one leaves the coast. Included in the table are monthly rainfall at Mundabullangana for 1960-62 and the monthly means for 34 years (these data were kindly supplied by Mr G. W. Mackey, Deputy Meteorologist, Perth).

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TABLE 1

Mean daily maximum and minimum temperature (°F) and relative humidity (%) at Roebourne, and monthly rainfall (inches) at Mundabullangana

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Max. temp.	101	101	98	94	86	79	79	83	90	94	101	102
Min. temp.	79	79	77	71	64	58	55	57	61	67	73	77
Rel. humidity	52	53	55	46	48	51	47	48	41	43	42	47
Rainfall, mean	2.2	3.3	3.7	1.3	1.0	0.9	0.4	0.3	0.0	0.1	0.1	0.4
Rainfall, 1960	2.6	8.0	0.9	0.1
Rainfall, 1961	9.1	8.5	4.2
Rainfall, 1962	4.0	1.9	0.0	0.1	0.3	0.5	0.1

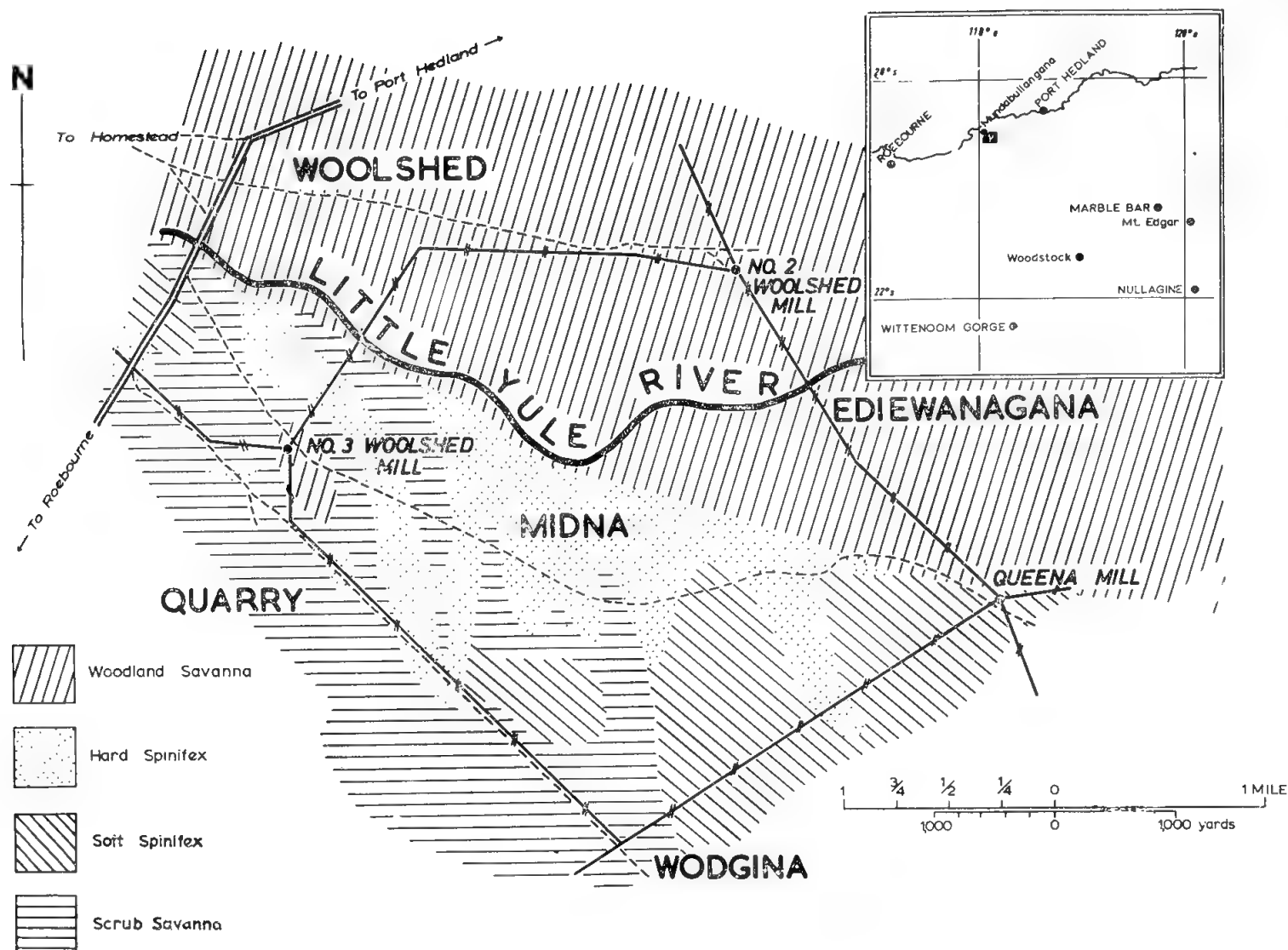


Figure 1.—Map of Midna and adjoining paddocks, Mundabullangana Station.

Vegetation

The vegetation of the area is divisible, from the viewpoint of kangaroo habitats, into four broad types: (1) Woodland Savanna, (2) Hard Spinifex, (3) Soft Spinifex, and (4) Scrub Savanna.

Woodland savanna occupies most of the country between the Yule and Little Yule Rivers, which themselves are lined with forests of river gum (*Eucalyptus camaldulensis*) and cajuput (*Melaleuca leucadendron*). Back from the rivers, the composition of the savanna depends on soil texture and frequency of inundation. Heavy, low-lying soils carry river gums and soft grasses (i.e. grasses other than *Triodia*), especially *Cenchrus*, *Eragrostis*, and *Eriachne* spp. As the land rises, cabbage gum (*Eucalyptus aspera*) and whitewood (*Atalaya hemiglauc*) become successively dominant, the principal grasses being buffel (*Cenchrus ciliaris*), birdwood (*C. setigerus*) and weeping grass (*Chrysopogon latifolius*). Finally on the lightest soils there only remain low trees of parkumara (*Owenia reticulata*), *Acacia sclerosperma*, kanji (*A. pyrifolia*) and corkwood (*Hakea lorea*). By this time the *Cenchrus* spp. have been largely replaced by soft spinifex (*Triodia pungens*) and spear grasses (*Aristida* spp.). Woodland savanna is the stronghold of the marloo, though the euro becomes increas-

ingly common in the drier and scrubrier parts of the savanna.

Hard spinifex occupies a considerable part of the study area south of the Little Yule. The soil is generally clayey, and the vegetation is dominated by *Triodia longiceps*, whose stiff pungent foliage is disdained by kangaroos and sheep. Its inflorescence, however, is surprisingly rich in nitrogen and provides good fodder in late summer. On the heaviest soils *T. longiceps* is replaced by another hard spinifex, *T. secunda*. Trees are absent and the only shrub present is the low, succulent *Trianthema turgidifolia*.

As the country becomes higher and the top-soil sandier, hard spinifex gives way to soft spinifex (*T. pungens*). Shrubs and low trees (especially kanji) begin to appear, but neither are as conspicuous as the great red termitaria of *Nasutitermes triodiae*. The dominant kangaroo here is the euro, which finds daytime shelter among isolated thickets of *Carissa lanceolata*, beneath the larger kanji, and occasionally in the shade of termitaria.

With increasing elevation and depth of sand, shrubs become numerous and varied, e.g. *Acacia translucens*, *A. holosericea*, *Pluchea tetranthera*, and *Cassia* spp. The dominant (and often the only) grass is *Triodia pungens*. There is a good variety of perennial herbs and low shrubs

(mainly leguminous and malvaceous), which however are only common where the spinifex has been checked. Since these herbs and low shrubs are much more palatable to sheep than the old tussocks of spinifex, their growth is induced by burning the spinifex, which itself is sought by sheep when young. The marloo is a sporadic visitor from neighbouring habitats and is found only on burnt areas. Euros are plentiful everywhere and have no difficulty in finding suitable daytime shelter in this zone of abundant shrubs and low trees.

In the foregoing account only perennial elements of the vegetation have been noticed. During and after good summer rains (as in 1961) there is much annual herbage, especially grasses, the commonest of which are *Dactyloctenium radulans*, *Eragrostis brownii*, *E. xerophila*, *Eriachne aristidea*, *E. obtusa*, *Xerochloa laniflora*, *Ichnanthus australiensis*, *Paspalidium clementii*, and *Perotis rara*. Moreover, such perennial grasses as *Chrysopogon latifolius* and *Cenchrus* spp., which may be reduced to little more than their rootstocks by the end of the dry season, rapidly resume their growth until much of the riverain country looks like a wheat-field. Dicotyledons are only conspicuous where the ground has been relatively bare, as around mills or in burnt country. The commonest species are *Commelina ensifolia*, *Trichinium obovatum*, *Gomphrena canescens*, *G. affinis*, *Ptilotus murrayi*, *Boerhaavia diffusa*, *Mollugo molluginis*, *Calandrinia creethae*, *Portulaca oleracea*, *Cleome viscosa*, *Tephrosia bidwillii*, *Euphorbia australis*, *E. atoto*, and *Seddera media*.

Movements and habitat preferences of the kangaroos

The study area was visited in February, May, August and November 1961. On each trip kangaroos (euros and marloos of both sexes and all ages after weaning) were sought in the evening with a spot-light and shot from a vehicle with a 0.26 inch rifle fitted with telescopic sights. Three standard routes were traversed at least twice each trip: (1) the northern track (from the highway eastwards to No. 2 Woolshed Mill,

thence southeastwards along the Midna-Edie-wanagana boundary for half a mile); (2) the middle track (from the highway southeastwards to Queena Mill via No. 3 Woolshed Mill; and (3) the southern track (along the southwestern boundary of Midna to the extreme southern corner of the paddock). The northern track was traversed on additional occasions to build up marloo samples.

When an animal was shot, it was dragged to the vehicle, sexed, and weighed. Next day its location when last feeding (marked temporarily the previous evening) was fixed, usually by compass triangulation to one or more mills. A one-chain transect was made at the location so as to obtain the percentage cover of perennial vegetation. In addition, all plant species, annual and perennial, within a 2-chain radius of each location were noted and the degree to which they had been grazed.

Results.

Table 2 gives the distance of kangaroo locations from nearest mill, and Tables 3 and 4 the density and composition of the plant cover.

TABLE 2

Mean distance (yards) of kangaroo locations from nearest mill. The figures in brackets are the percentage of locations within half a mile of a mill

	Euro	Marloo
February	1440 (39)	1780 (26)
May	1070 (54)	840 (50)
August	1230 (44)	570 (81)
November	990 (43)	590 (86)

TABLE 3

Mean percentage (by area) of perennial cover and bare soil* at euro locations. Marloo data in brackets.

	Perennial Cover	Bare Clay and Clayey Loam	Bare Sand and Sandy Loam
February	26 (22)	17 (40)	57 (38)
May	20 (15)	16 (35)	64 (50)
August	18 (17)	10 (27)	72 (56)
November	21 (8)	19 (41)	60 (51)

* Bare soil includes ground carrying ephemeral vegetation.

Remarks

Since the mean distance from the nearest mill of all points on the traverses was 1490

TABLE 4

Mean percentage composition (by area) of perennial ground cover at euro locations. Marloo data in brackets.

	January	May	August	November
Grasses				
<i>Cenchrus</i> spp.	14.3 (53.6)	32.8 (48.9)	24.9 (51.6)	45.2 (22.1)
<i>Chrysopogon latifolius</i>	2.7 ()	4.5 (4.2)	0.7 ()	1.4 (3.3)
<i>Eragrostis</i> spp.	— (2.2)	(3.3)	(20.3)	0.3 (12.5)
<i>Eriachne</i> spp.	}			
<i>Triodia longiceps</i>		1.3 (9.7)	13.7 (1.1)	2.1 (5.0)
<i>Triodia pungens</i>		48.8 (29.0)	54.8 (24.0)	42.3 (39.2)
<i>Triodia secunda</i>	1.2 (3.9)	0.4 ()	()	(3.3)
Total grasses	86.8 (95.2)	87.8 (95.1)	94.1 (97.0)	91.3 (85.4)
Herbs and Shrubs				
<i>Acacia</i> spp.	1.4 ()	3.1 ()	0.4 (0.4)	0.9 ()
<i>Aerva javanica</i>	— (0.2)	— ()	— ()	— (1.1)
<i>Bonamia rosea</i>	— ()	0.3 ()	— (0.4)	0.2 (5.6)
<i>Cassia</i> spp.	1.5 ()	1.8 (1.1)	1.7 (0.4)	0.7 (5.6)
<i>Corchorus walcotti</i>	3.1 ()	3.7 (1.2)	2.4 ()	5.4 (0.6)
<i>Ipomoea muelleri</i>	0.3 ()	0.9 (2.4)	— (0.7)	0.3 ()
<i>Pluchea tetranthera</i>	3.0 ()	1.9 ()	0.8 (1.1)	0.5 ()
<i>Trianthema turgidifolia</i>	1.4 (3.7)	— ()	— ()	— ()
Other species	2.5 (0.9)	0.5 (0.2)	0.6 ()	0.7 (1.7)
Total dicots	13.2 (4.8)	12.2 (4.9)	5.9 (3.0)	8.7 (14.6)

yards, it is clear from Table 2 that the kangaroos were distributed in February (in contrast to other seasons) independently of the mills. At first sight this independence may seem to have been due alone to the wide dispersal of water—the Little Yule was flowing and all claypans were filled, so that the mean distance from nearest water of marloo and euro locations was 200 and 340 yards respectively; whereas in subsequent trips the nearest water to almost all animals was in fact at the mills. However, the situation was not as simple as that, and the implication that marloos were more dependent than euros on mill water was not supported by other observations.

In February a considerable proportion of the marloos were obtained on the middle track at large claypans between No. 3 Woolshed and Queena Mills (hence the high mean distance of locations from nearest mill). They were feeding on the lush growth of annual grasses round the edge of the water. By May the water had disappeared and also all the herbage, and no marloos were obtained there during that or later trips. There was simply little suitable food for them in an area where the vegetation in the dry season consisted mostly of hard spinifex.

As the data in Tables 3 and 4 indicate, the marloo prefers sparsely vegetated country and especially the heavier soils which support soft grasses rather than *Triodia pungens* and scrub. It shuns the latter, except where after a burn there is a regeneration of young grasses and herbs. It so happens that conditions favourable to marloos are more often encountered near mills than distant from them. The concentration of watering sheep round mills inhibits the growth of scrub; and the bare, heavily manured soil favours *Cenchrus* over *Triodia*. Controlled burns, out of consideration for the sheep, are carried out in scrub and *Triodia pungens* within easy walking of mills. Thus the apparent drift of marloos towards mills in the dry season could be attributed to the shrinking of the food supply as well as to that of water.

The average distance of euro locations from mills was inflated in February by the large numbers taken towards the southern corner of Midna paddock, where the vegetation consisted mostly of old unburnt *Triodia pungens*. In

February the *Triodia pungens* was flowering and provided the euros with abundant fodder. Later in the year when the inflorescences had gone and the foliage had become resinous, the euros increasingly turned to other sources of food. Again, it is hard to separate the effect of availability of water from that of food when interpreting the general dry-season withdrawal of animals to the vicinity of mills. Whatever their causes, these movements brought the two kangaroos (and sheep) into closer contact towards the end of the year.

Composition of the diet

A sample of faeces was taken from the rectum of each kangaroo that was shot. The vicinity of all kangaroo locations was searched for fresh sheep faeces; if present, one or two samples were collected, each apparently from a single animal. These were augmented with material from grazing flocks, whether or not they were at a kangaroo location. On returning to Perth, faecal samples were dried, ground, prepared into slides and examined microscopically as in Storr (1961).

Since grass was the major component in the diet of all three animals, it was desirable to identify grass epidermis to species. Generally it was not difficult to identify grasses to genus; but because intra-specific variation in epidermal characters often overlapped that between congeneric species, identification depended unduly on the knowledge of what was present at each location. Moreover, the animals were obviously eating some species (usually identifiable to genus) that were not collected by the writer. Most of the data have therefore been lumped under genera.

The identification of dicotyledons posed even greater problems, not because of intrinsic difficulties, but because their great variety (out of all proportion to their dietary importance) precluded the preparation and study of all but a fraction of the items eaten. This deficiency mainly affects the sheep data, which for other reasons are not so reliable as those for the kangaroos. Apart from the different way of sampling the sheep, particles in their faeces were so small as to render their identification and quantification difficult and uncertain.

Results

See Table 5.

TABLE 5
Mean percentage composition (by area of epidermis in faeces) of the diet of kangaroos and sheep

	February			May			August			November		
	Euro	Marloo	Sheep	Euro	Marloo	Sheep	Euro	Marloo	Sheep	Euro	Marloo	Sheep
<i>Aristida</i> spp.	1	...	0	11	2	8	22	13	5	33	29	1
<i>Cenchrus</i> spp.	7	30	42	20	25	21	32	54	37	34	34	37
<i>Chrysopogon latifolius</i> ...	11	14	3	7	6	13	4	3	1	4	4	6
<i>Dactyloctenium radicans</i> ...	1	26	5
<i>Eragrostis</i> spp.	3	6	9	2	9	1	0	6	1	0	3	1
<i>Eriachne</i> spp.	1	3	10	12	4	4	2	4	1	1	3
<i>Ichnanthus australiensis</i> ...	0	0	9	1	2	1
<i>Paspalidium clementii</i> ...	2	3	12	1	1	0
<i>Perotis rara</i>	1	4	2
<i>Triodia</i> spp.	70	12	7	30	17	11	31	11	17	19	12	15
Other grasses	1	2	1	1	1	0	0	1	0
Non-grasses	2	3	7	18	26	41	7	10	35	9	15	37

Remarks

In February, food and water were so abundant and widely dispersed that the kangaroos and sheep could exercise their food preferences without restraint. As a result, they tended to segregate, even though all three species were feeding largely on grasses. The euros were mostly eating *Triodia* (especially their inflorescence); the marloos, *Cenchrus*, *Dactyloctenium* and *Chrysopogon*; and the sheep *Cenchrus Paspalidium* and *Eragrostis*. The fact that *Cenchrus* was the major food item of both marloos and sheep was unimportant, for there was far more of it than either of them could eat.

Most of the annual grasses that came up with the January rains (e.g. *Dactyloctenium*, *Paspalidium*, *Perotis* and *Eriachne japonica*) had disappeared by May, when a new but smaller crop was maturing (e.g. *Aristida* spp. and *Eriachne aristidea*). Meanwhile the spinifex inflorescences had withered away and the leaves of *Triodia pungens* in the absence of rain had become coated with resin. The euros were eating much less *Triodia* than earlier and much more *Cenchrus* and such dicots as *Bonamia rosea* and *Hybanthus enneaspermus*, as well as sharing with the sheep and marloos the new crop of annual grasses. The change in diet of the marloos was smaller; it was partly brought about by the increased number of animals on spinifex burns, which resulted in greater consumption of dicotyledonous herbage (especially *Bonamia*) and young *Triodia pungens*. The sheep undertook a similar but more marked shift to burnt country, where they ate a much wider variety of dicots than either of the kangaroos.

Despite the dwindling supply, consumption of *Cenchrus* by all species increased in August. Both kangaroos, but not sheep, were eating more spear grass (*Aristida*) and less dicotyledonous herbage, which was then becoming scarce on the spinifex burns.

By November the euros were hardly eating more spinifex than were the marloos and sheep. Indeed all three species were perforce eating much the same things. The only considerable differences were the small intake of spear grass by sheep and their large intake of dicots. Few of the latter were specifically identified in faeces, but observations indicated that in early summer the sheep were increasingly browsing *Atalaya hemiglaucula* and kapok (*Aerva*). Though neither of these was eaten much, if at all, by kangaroos, there can be little doubt that they were seriously depriving the sheep of other sources of food in the last few months of the year. While most plants of *Cenchrus* had grown rank and finally withered away, a few of them had been grazed low all the year; and where the water supply was better than usual, as between wheel tracks and at mill overflows, there was a more or less continuous growth of fresh foliage. However, the demand towards the end of the year for these last remaining sources of green grass was excessive, and they were rapidly depleted.

Nitrogen and water content of food

On each trip at least 20 g (dry weight) of terminal foliage was collected from five or more individual plants of all species known to be eaten in substantial amounts. The samples were weighed in the field to the nearest 0.5 g, and again in Perth after oven-drying to constant weight. The material was then ground and analysed for nitrogen by the Kjeldahl method, as modified by Willits, Coe and Ogg (1949).

Nitrogen and water content were applied to the dietary data (summarised in Table 5) to give the mean nitrogen and water content of each species' total ingesta.

Results

See Tables 6 and 7.

TABLE 6
Nitrogen content (% dry weight) of major food items
Water content (% wet weight) in brackets

	February	May	August	November
Grasses				
<i>Aristida</i> spp.	0.7 (41)	0.7 (39)	...
<i>Cenchrus</i> spp.	1.4 (82)	1.4 (61)	1.3 (64)	0.8 (31)
<i>Chrysopogon latifolius</i>	1.6 (80)	0.8 (61)	0.8 (48)	0.9 (42)
<i>Dactyloctenium radicans</i>	1.5 (81)
<i>Eragrostis</i> spp.	1.7 (65)	0.6 (38)	0.5 (14)	0.7 (14)
<i>Eriachne</i> spp.	1.7 (72)	0.9 (37)
<i>Paspalidium clementii</i>	2.5 (87)
<i>Triodia longiceps</i>	1.4 (55)	1.0 (28)	1.2 (39)	0.8 (17)
<i>Triodia longiceps</i> (I)	1.9 (59)
<i>Triodia pungens</i>	0.8 (51)	0.8 (51)	0.5 (22)	0.7 (14)
<i>Triodia pungens</i> (I)	1.1 (44)
<i>Triodia pungens</i> (S)	0.9 (52)	...	0.6 (37)
<i>Triodia secunda</i>	1.6 (71)	1.5 (48)	1.7 (44)	1.3 (29)
<i>Triodia secunda</i> (I)	1.4 (56)
Non-grasses				
<i>Aerva javanica</i> ..	1.7 (74)	1.6 (40)	1.3 (56)	1.8 (67)
<i>Atalaya hemiglaucula</i>	1.6 (63)
<i>Bonamia rosea</i>	1.8 (53)
<i>Hybanthus enneaspermus</i>	1.5 (63)
<i>Leguminosae</i> *	2.8 (69)	2.0 (58)	1.1 (34)

I, inflorescence; S, seedlings.

* Average of *Crotalaria crispata*, *C. trifoliatum*, *Indigofera monophylla*, *Psoralea martini*, and *Tephrosia bidwillii*.

TABLE 7

Nitrogen content (% dry weight) of ingesta.
Water content (% wet weight) in brackets.

	Euro	Marloo	Sheep
February	1.3 (62)	1.6 (77)	1.7 (79)
May	1.1 (55)	1.2 (57)	1.2 (60)
August	1.0 (48)	1.1 (53)	1.2 (54)
November	0.8 (31)	0.8 (30)	1.0 (37)
Year	1.0 (49)	1.2 (54)	1.3 (58)

Remarks

From maxima in February, the nitrogen and water content of herbage generally decreased throughout the year. The decline in nutrients was most pronounced in soft grasses, somewhat less in *Triodia*, and least in dicots.

The sheep, feeding almost exclusively on soft grasses in the wet season and to a large extent on dicots in the dry season, maintained throughout the year a level of nitrogen and water intake (from herbage) that was about 20% greater than in euros. In both respects the marloos were usually intermediate—somewhat nearer to the sheep in the first half of the year, and nearer to the euros in the second. Of the three species the marloos thus experienced the sharpest decline in nutrient levels, e.g. a 48% drop in nitrogen between February and November.

Daily intake of dry matter by kangaroos

The principle behind the method described below is that in Storr (1963), viz. that daily intake is on average equal to daily loss of dry matter from the stomach. But owing to the difficulty of catching and holding kangaroos alive, it was necessary to modify the procedure used with *Setonix*.

Adult kangaroos of a given species and sex were shot in the early morning after they had ceased to feed, and again in the afternoon before they resumed feeding (the mouths of shot animals were searched for feed, so as not to include in samples any animals that were feeding). Entire stomachs were dissected out and preserved in 44-gallon drums of 70% alcohol. In Perth the stomachs (and their contents) were oven-dried to constant weight.

Assuming (1) a linear rate of loss of dry matter from the stomach, and (2) no difference between samples in mean weight of stomach (exclusive of contents), the difference in mean dry weight of stomach plus contents between morning and afternoon samples was extrapolated to give the mean daily rate of loss from the stomach and the presumed intake of dry matter.

Male euros were sampled between 27 February and 2 March 1962, and female marloos between 26 October and 2 November 1962.

Results

See Table 8 and 9.

TABLE 8

Adult male euros: mean dry weight of stomach plus contents in morning and afternoon (standard deviations in brackets)

	a.m.	p.m.
Number in sample	6	7
Mean body weight (kg)	33.5 (2.2)	33.9 (2.6)
Mean time shot (hr and min)	08.20 (28)	05.41 (20)
Weight of stomach + contents (g)*	776 (84)	606 (67)
* Mean rate of loss: 170 g in 9.35 hours, i.e. 436 g/day.		

TABLE 9

Adult female marloos: mean dry weight of stomach plus contents in morning and afternoon (standard deviations in brackets)

	a.m.	p.m.
Number in sample	9	10
Mean body weight (kg)	23.5 (3.4)	22.4 (2.0)
Mean time shot (hr and min)	06.49 (42)	5.08 (36)
Weight of stomach + contents (g)*	617 (72)	497 (89)
* Mean rate of loss: 120 g in 10.33 hours, i.e. 279 g/day.		

Remarks

For the comparison of metabolic phenomena, including DMI (daily dry matter intake), between animals of different size, Brody (1945) recommended adjusting for body weight not directly but by the power of 0.73. Thus DMI in the adult male euros was 33.6 g/kg $W^{0.73}$, a value that agrees well with that observed in captive euros. Six females (mean weight 12.7 kg) had a mean DMI of 231 g (Brown, 1964), which is equivalent to 34.5 g/kg $W^{0.73}$. A male euro (weight 17 kg), kept by Ealey (pers. comm.) at Woodstock (120 miles southeast of Mundabullangana) and fed on buffel grass (averaging 44% water and 0.7% nitrogen), had a mean DMI of 259 g, i.e. 32.7 g/kg $W^{0.73}$.

DMI in the adult female marloos at Mundabullangana was only 28.4 g/kg $W^{0.73}$. Ealey also observed a low DMI in a young marloo (10 kg) at Woodstock. Fed the same diet as the euro cited earlier, its DMI averaged 126 g, i.e. 23.5 g/kg $W^{0.73}$. Nevertheless it is doubtful whether marloos generally have a lower intake than euros. First, Brown (1964) obtained much the same values in the two species. Second, the Woodstock marloo was upset by the experiment (Ealey pers. comm.). Third, the low intake observed by me was probably due to drought conditions. Of all adult female kangaroos examined in October–November 1962 (euros as well as marloos) only one had a furred joey in the pouch. All other joeys were small and naked, and juveniles at heel were fairly large. Evidently the diet then and for some time previously was inadequate for producing milk beyond the requirements of small joeys. Sadleir (1961) observed no such failure to rear joeys to weaning in the two years of his fertility studies at Mundabullangana, but then neither of those years (1960 and 1961) was so dry as 1962. Moreover, spring 1962 was abnormally hot.

While it is unlikely that DMI is generally lower in marloos than euros, it is probably much lower in kangaroos than sheep. Fels, Moir and Rossiter (1959) investigated the organic matter intake (i.e. dry matter less ash) in six merino wethers at Kojonup in the southwest of Western Australia. On a grass-dominated pasture, daily intake remained fairly steady from September to December, the mean rate being 55 g/kg $W^{0.73}$. On a clover-dominated pasture mean daily intake declined from 78 g in September to 51 g in October and 40 g in December. The intake of sheep under the very different conditions in the Pilbara could well be lower, but hardly so low as to justify the popular belief that a kangaroo eats twice as much as a sheep.

Seasonal changes in body weight of kangaroos

Kangaroos continue to grow after attaining sexual maturity. As small samples such as these may vary considerably in age structure, mean weight alone does not accurately reflect seasonal changes in weight. For example, the large increment in August 1961 of young adult female marloos completely masked the general weight gain over the previous three months. Some allowance must therefore be made for inter-sample differences in real size of animals. Unfortunately pes length, the only linear measurement taken, is poorly correlated with real size. Male euros, for instance, have been examined with almost the same pes length but

differing by 14 kg in weight. Growth in adult females is much slower than in males, so that inter-sample differences in real size are small and observed weights require little adjustment.

The overall mean pes length of adult female marloos and euros was 291 and 247 mm respectively. Observed weight has been adjusted to these lengths, using the relation established by Sadeir (1961) between pes length and body weight in large samples of Mundabullangana kangaroos. For ease of comparison, mean adjusted weight of each sample has also been expressed as a percentage of the weight in August.

Results

See Table 10.

TABLE 10
Weight of adult female euros in 1961, with marloo data in brackets

	February	May	August	November
Number in sample	17 (13)	19 (14)	12 (9)	16 (13)
Mean pes length (mm)	249 (296)	247 (292)	247 (283)	246 (287)
Mean obs. weight (kg)	14.4 (20.5)	14.9 (22.7)	16.4 (22.5)	15.7 (22.4)
Mean adj. weight (kg)	14.2 (19.6)	14.9 (22.6)	16.3 (23.5)	15.8 (22.9)
Index	87 (83)	92 (96)	100 (100)	97 (97)

Remarks

The weight of the kangaroos in 1961 was probably lowest in early January, at the onset of the summer rains. Even after three or four weeks good feeding, weights were still very low in February and much lower than in other trips. Dry season weight losses could thus amount to 20%.

Though the samples are not really adequate for interspecific comparisons, the marloos apparently put on weight quicker than the euros. This could well have been so; for the soft grasses, which constituted the greater part of their late summer diet, were not only superior in nitrogen to the euros' fare, but undoubtedly also in energy and digestibility.

Between August and November both species lost only 3% of their weight, despite the complete lack of rain since the preceding March and the continuous decline in nutrients. Euros began to lose weight only when the nitrogen content of their food fell below 1%, or in other words, when the daily intake of nitrogen was less than 330 mg/kg $W^{0.73}$. This value is close to G. D. Brown's estimate of the euro's minimal requirements of dietary nitrogen under experimental conditions, viz. 309 mg/day/kg $W^{0.73}$ (Brown, 1964).

Discussion

The various aspects of this research have been discussed in the body of the paper. It now remains to assess their significance in the total Pilbara scene. Before doing so, it will be helpful to recapitulate the present results and to indicate how their generality may be limited by peculiarities of time and place.

Recapitulation

The rains of January-March 1961 were very much above average. Surface water was abundant and widespread, as were annual grasses, ephemeral herbs and rejuvenating perennials. Euros, marloos and sheep were largely segregated as they freely exercised their food preferences.

No rain fell in 1961 after March, and surface waters had disappeared by early May. Herbage, however, remained fairly plentiful until early winter, and the kangaroos did not lose weight till after August.

The variety, quantity and quality of palatable herbage continually declined throughout the last six months of 1961. The decline was least severe in the vicinity of mills, where (1) on heavier soils, trampling by sheep had suppressed spinifex and shrubs in favour of the introduced buffel and birdwood grasses; and (2) on lighter soils, the burning of old spinifex had stimulated the growth of a wide variety of forbs and soft grasses and of seedling *Triodia pungens*.

Throughout the year marloos maintained their preference for clayey plains sparsely vegetated with soft grasses, and euros for sandier country vegetated more densely with spinifex and shrubs. Nevertheless the contraction of the food supply resulted in increasing overlap between the diets of the two species of kangaroo, till in November there was no great difference between them. While the diet of the sheep showed a trend towards those of the kangaroos, there was still considerable disparity in November, when the sheep were eating much more browse than the kangaroos but very little spear grass (*Aristida* spp.).

In 1962, a much drier year, field estimates were made of the daily intake of dry matter by the two kangaroos. Adult male euros averaged 33.6 g/kg body-weight in February-March, and adult female marloos 28.4 g/kg in October-November (at a time when they and female euros were prevented by drought from rearing their pouch-young).

Peculiarities of time and place

Certain things limit the generality of the above results both for Mundabullangana and for the Pilbara as a whole. First, the dietary studies were carried out in an unusually good year. Several of the annual plants that were common in February 1961 were not seen by

Mr A. S. George (State Herbarium) when he accompanied us on Mundabullangana twelve months later. It seems likely, then, that in many wet seasons the diets would comprise fewer items than in 1961 and there would be less disparity between sheep and kangaroo diets, as well as less physical segregation between the animals.

Second, and more important, the present study area is typical of only a small portion of the Pilbara, viz. the best parts of the coastal plain and of the lower valley of the De Grey River (see map, Anon. 1962). Mundabullangana, in fact, lies at one end of a scale whose other extreme is well exemplified by Mt. Edgar, 25 miles southeast of Marble Bar and one of the study areas of Sadleir (1965) and of Ealey, Bentley and Main (1965).

The country at Mt. Edgar, though less hilly than its surroundings, has considerable relief, and its soils are largely skeletal. Hence much of the water from heavy rains is discharged via numerous gullies and creeks into the Talga River. In contrast, the deeper and loamier soils of Mundabullangana are greatly superior in their capacity for holding moisture, and because of the gentle topography drainage channels are poorly developed. Excess water gravitates to local hollows and low-lying plains; relatively little of it flows into the Yule and Little Yule Rivers. Consequently the seasonal distribution of rain is not so important here as at Mt. Edgar. As we have seen, there was sufficient soil moisture at Mundabullangana for the production in autumn and winter 1961 of abundant herbage on spinifex burns, even though no rain fell after March.

The climate, too, is more favourable on the coastal plains than in the interior. Daily maximum temperature at Roebourne averages 4-6°F lower than at Marble Bar in the period October-March, and throughout the year relative humidity is considerably higher at Roebourne. Conditions are thus more favourable for dew, which at Mundabullangana may alone suffice for continuous growth in scattered, heavily grazed tussocks of birdwood and buffel grass.

Conclusions

The following conclusions, I believe, will hold for most years and most parts of the Pilbara.

1. The quantity of nutrients available to sheep and kangaroos varies from year to year according to rainfall and management. Within a year the quantity generally declines from the end of one summer to the beginning or middle of the next. This decline may be locally arrested by either winter rain or the retention of soil moisture.

2. Of the two kangaroos, the marloo is dietetically the nearer to sheep. This is probably the main reason for marloos being resident and plentiful only in the better sheep country, viz. zone A of Anon. (1962). In the remainder of the Pilbara the marloo is a rare vagrant.

3. One of the principal differences between marloo and sheep diets is the much higher incidence in the latter of dicotyledonous forage. A similar disparity between marloo and cattle diets was observed by Chippendale (1962) in Central Australia.

4. Spear grasses of the genus *Aristida* constitute a major dry-season item in the diet of

kangaroos, whereas sheep seldom eat these grasses when dry. Similarly in Queensland (Kirkpatrick, 1965), grey kangaroos (*Macropus giganteus*) commonly eat *Aristida* spp., all of which are relative unpalatable to sheep.

5. Of the three diets, the euro's includes the most spinifex and the least dicotyledonous herbage. This is probably why the euro alone prospers in the rougher parts of the Pilbara, where spinifex overwhelmingly dominates the vegetation.

6. Though the three species are clearly differentiated in their food preferences, there is usually too little food for the free exercise of these preferences, and large dietary overlaps are inevitable. While kangaroos clearly eat food that would otherwise be available to sheep, neither the present research nor any other indicates the effect of this competition on the Pilbara wool industry.

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